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ORTHOGENESIS

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ORTHOGENESIS FROM THE STANDPOINT OF THE BIOCHEMIST

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It does not seem likely that physical science should have much to say about the theory of orthogenesis. In the first place, it is hard to see what the term means if one adopts a physico-chemical standpoint. In the second place, organic evolution is more remarkable in its morphological aspects than in its chemical and physico-chemical aspects.

I

The first point may be dismissed with a few remarks. Orthogenesis presumably means that evolution has taken place in a straight line or in a very restricted path, and that the straightness of the line depends, at least partly, upon something which is internal to the organism, though, of course, the process may be released by a stimulus from the environment. The straightness of the process must be largely a matter of definition. Physico-chemically, it could hardly mean more than that quantitative changes have steadily the same sign over a considerable period of time.

One might, perhaps, adopt such a view, if one could believe, as has been often suggested, that variation is the expression of a process which is approaching a condition

of equilibrium, because then, so far as there is no unto-ward interference from without, it would be natural to think that the course of the process must be in a certain sense a straight one, with a negative acceleration. Taken literally, such a consideration is, however, purely speculative and for the present, I think, a sterile speculation.

Somewhat more clearly intelligible is a hypothesis which arises from the study of hormones and their rôle in development. It appears to be quite possible that the effect of increase or decrease in the amount of a single chemical substance in a species might be a complex change in its structure, including modifications of size, of the proportions of the different parts, of pigmentation, or of the other peculiarities which ordinarily arrest the attention of students of evolution. This would be especially true if, instead of a change in the amount of a hormone or other substance, it were a case of the formation of a new compound. Such changes, while directly due to a single substance, might be greatly modified by readjustments following the disturbances of the physiological equilibria between the different parts of the body. Compensatory readjustments of similar nature are, of course, among the most familiar and interesting phenomena in pathology. We are, accordingly, fully justified in taking their possibility for granted.

It is, therefore, conceivable that evolutionary changes should be occasionally progressive and apparently orthogenetic, although due to a simple physico-chemical modification. No doubt, if it were desirable, such considerations might be developed into a clear and possibly useful theory of orthogenesis, but I am not qualified to do so. My object is only to insist that changes which from a morphological standpoint are complex, continuous, and progressive, may conceivably be due to a single, simple, physico-chemical change.

Such reflections, vague though they may be, clearly point to a conclusion which is, I feel sure, inevitable for the physical scientist; morphological phenomena in them-

selves are not sufficient to establish the validity of any theory of the mechanism of evolutionary variation.

II

More important than speculating about such questions is the fact that the underlying physico-chemical processes in living organisms seem to have remained about the same throughout the whole process of evolution. So far as it is possible to form any opinion on the matter, this conclusion is inevitable.

In considering the question of organic evolution it should always be remembered that, with very trivial exceptions, the economy of life on the earth is now and probably always has been founded upon the synthesis of carbohydrates from water and carbonic acid with the accompanying fixation of energy, followed by the conversion of carbohydrates into fats, proteins, and a great variety of other related substances. Later there is an oxidation of these substances back to water and carbon dioxide, accompanied by the utilization of the energy in various forms of organic activity. Correlated with this is the fact that cells are made up of water, carbonic acid, carbohydrates, fats, proteins, and certain other substances. They are enough alike in chemical composition and in physico-chemical structure fully to justify the concept of protoplasm as a fairly constant physico-chemical apparatus throughout the organic world.

These familiar facts of chemical physiology and chemical morphology undoubtedly depend upon the properties of the substances involved. Water and carbonic acid, with which the process begins and ends, and which seem to be everywhere the foundation of protoplasm, possess in themselves such a large number of remarkable characteristics and lead directly through the formation of sugars to such a great variety of chemical substances and chemical reactions, that it is hard to believe in the possibility of the existence on a large scale of any very different kinds of living organisms.

This is a subject that I have elsewhere discussed at length. Hence it will perhaps suffice briefly to recapitulate a few of the more striking facts. Because of its peculiarities as a solvent, as an ionizing medium, etc., water makes possible the formation of an almost indefinitely greater variety of physico-chemical systems than does any other substance. On account of its high latent heat of vaporization, its high specific heat, its high surface tension, and the peculiarities of carbonic acid, such systems often possess a very remarkable stability. The elements hydrogen, carbon, and oxygen, of which water and carbon dioxide are composed, seem to be unique in the number and variety of the substances which they can form. In particular, the production of sugar from water and carbon dioxide fixes a very great amount of energy and leads directly to the greatest variety of chemical substances and reactions which are known to occur as the result of one chemical process. Finally, water and carbon dioxide are the two substances which are everywhere available.

Anything so complex, so stable and yet so variable, so widespread and so active as life can only occur when a great variety of conditions are fulfilled. In other words, the physico-chemical systems of the organism, in order that life shall be capable of its evolution, must possess altogether exceptional characteristics, which appear to be quite impossible unless water and carbonic acid, and compounds of the three elements, hydrogen, carbon, and oxygen, and no doubt also of nitrogen, are at the basis of them. These substances possess a set of properties each one of which by itself and also in cooperation with the others is necessary for the highest physico-chemical complexity and variability. So far as we know, no other elements or compounds possess another set of properties which permit similar physico-chemical complexity or variability.

It is, I believe, for this reason that life has always operated on the same basis.

Thus while the evolutionary process has certainly produced a large number of well-defined series of changes when it is looked at from the morphological point of view, it still remains very probable that such physico-chemical changes as have occurred are not only of a secondary nature, but that they are much less of the character of serial modifications. Indeed, one is tempted to say that in a physico-chemical sense, the variations are distributed in rather a random manner, without any particular indication of a general progressive tendency, such as we seem obliged to think of in studying morphological variation.

No doubt the evolutionary process has, from time to time, invented new chemical substances and greatly modified colloidal systems. In the total these changes are very numerous and of the utmost importance to the student of evolution. But *progressive* change is more particularly a morphological phenomenon and it seems to be almost self-evident that progressive morphological evolution should not be accompanied by the same degree of continuous variation in straight lines in physico-chemical properties. Such a parallelism would, I think, be well nigh unaccountable. However that may be, there is no evidence for it.

III

Another consideration which makes the theory of orthogenesis seem very different to a physical chemist from what it must seem to a biologist, is the fact that chemistry tends to deal with individual substances which either exist or do not exist. The case of hemoglobin will illustrate this point. Hemoglobin is an individual substance of very marked peculiarities. So far as known there are no essential differences between the hemoglobins contained in the bloods of different species. It is possible that the known differences in crystal form depend upon something more than trivial differences in the amino acids which make up the molecule, but this seems unlikely. In any case, it will do no harm to speak of hemoglobin as

a single chemical individual in order to illustrate a particular point.

This substance is the sole means of transporting more than a small amount of dissolved oxygen in the blood of those species which contain it. It is, therefore, apparent that it may be thought about from the evolutionary point of view, much as one thinks about an organ. I believe that the success of Aristotle's system of classification justifies this view. But while it is easy to think of the gradual evolution of an organ as something which can not be regarded as appearing at any point in the evolutionary process, being related by a process of continuous differentiation to something which was certainly not the same organ in an ancestral species, there is not the slightest evidence for anything of the sort in the case of hemoglobin, and it must seem to most chemists nothing less than fantastic to assume such a continuous evolution of a substance more and more closely approaching hemoglobin. Moreover, it is almost as difficult to imagine such a thing from the standpoint of a biologist, and it is certainly true that any given organism either does or does not contain a substance which is capable of forming a loose chemical combination with oxygen.

But the difficulty in the case of hemoglobin is more serious than this, for it has been found that hemoglobin, like other organs, has more than one function. It has, in fact, at least three; for it is the sole means of transporting oxygen, almost the sole means of liberating carbonic acid in the lung and absorbing it in the tissues, and the instrument of the final delicate adjustment of the alkalinity of the blood. The last two functions depend upon the same property in the hemoglobin molecule, but this property is a different one from that which enables hemoglobin to combine with oxygen. We are, therefore, here confronted with the task of imagining the origin of a chemical substance, quite different in its nature from any other known substance, which possesses two chemical peculiarities, and which, as a result of these two peculiarities, performs three highly important functions.

Now it may be that originally hemoglobin possessed only one of these peculiarities, so that its sole original function was to carry oxygen. And accordingly one of the most interesting questions of comparative physiological chemistry concerns the respiratory function of the blood. It would be a very important discovery to find a kind of hemoglobin in which there is no specialized action upon the transport of carbonic acid and upon the alkalinity of the blood. But even if the earliest hemoglobin were of such a nature, the first production of hemoglobin would still seem to have been relatively an extremely discontinuous variation involving an unmistakable physiological unit of great importance.

It is true, and should be noted in order to avoid confusion, that there has been a later evolution of the process of oxygen transport. This has been commented on by Barcroft as a result of his own important researches. It appears that variation in the electrolytes of the red cells is accompanied by remarkable variation in the affinity of their hemoglobin for oxygen, and that this is the explanation of the differences in the so-called oxygen dissociation curves of the bloods of different species of mammals. Here, as Barcroft points out, there is no difficulty in imagining a process of adaptation, for the fact of chemical discontinuity is not involved. It is a question of changing proportions of the different substances.

But in spite of the possibility of such phenomena, it seems probable that there are, even in the human species alone, a considerable number of important individual substances whose appearance in the course of organic evolution it is very difficult to imagine, except as a radical innovation.

Accordingly, it must be apparent that in the present state of our knowledge, any theory which postulates continuity in evolution is very unsatisfactory to the chemist.

Moreover, in this case one seems to be confronted with an appearance of discontinuity which does not depend, as is too often the case, upon a judgment of the magnitude of a difference.

Of course, it is not difficult to imagine a sufficiently close approach to continuity of evolution, and therefore, to orthogenesis, in the case of simple proteins. But here, very likely on account of our ignorance, there is no indication of anything more than indefinite variation and variability, accompanying variation in a definite direction in the morphological characteristics of species.

On the whole, variation in the ultimate physico-chemical nature of organisms seems to have been rather discrete than continuous, not orthogenetic, but distributed at random. Such a conclusion may possibly be illusory, for our ignorance is greater than our knowledge. But whatever the nature of the changes which it has undergone, the most striking thing about the physico-chemical nature of protoplasm seems to be its uniformity throughout nature.

Therefore, with due reservations because of the incompleteness of bio-chemical knowledge, it seems reasonable to suppose that apparent instances of orthogenesis may sometimes depend upon a single important chemical change in an organism, followed by slow and progressive modifications leading up to a definitive morphological result. Such a process would be somewhat analogous to the establishment of a condition of equilibrium.

ORTHOGENESIS IN BACTERIA

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It is well to understand at the outset that bacteria, unlike plants and animals, can not be studied from the orthogenetic standpoint in the strict sense, owing to the lack of a proper vantage point, or, perhaps more correctly speaking, a basis from which one may start such a study. In my opinion, all attempts at the establishment of systems of bacteria, and there have been many, have ended in creating greater confusion than there was at the start. Such frustration of well-intentioned programs was inevitable for at least three reasons, to wit: (1) Every bacteriologist used criteria of his own for the establishment of new species. This is bound to lead to chaos. (2) Nearly all bacteriologists used a morphological basis for classification. Owing to the relative simplicity of form of bacteria, this must inevitably result in erroneous discriminations. (3) Nearly all bacteriologists in the past and even to-day are laboring under the misconception that bacteria are simpler forms of living organisms than they really are. That this is incorrect has been shown by the studies of Löhnis and Smith in 1916¹ and of Löhnis alone very recently.²

But assuming the foregoing to be true, it must follow that it is impossible to trace the evolution of new species of bacteria in a definitely directed course. Not being certain what constitutes a forward or what a backward step

¹ (a) "Life Cycles of the Bacteria," preliminary communication, *Jour. Agric. Res.*, Vol. 6, No. 18. (b) "Life Cycles of the Bacteria," paper read at New Haven meeting of Soc. Amer. Bacteriologists, Dec. 27, 1916.

² "Studies upon the Life Cycles of the Bacteria," Part I, Review of the Literature, 1838-1918, *Nat. Acad. Sciences*, Vol. XVI, Second Memoir.

in bacterial development, it is obvious that we can not apply as justifiably as we do in the case of the higher organisms the criteria of definitely directed evolution. To be sure, we have a number of instances of the establishment of permanent new characters in bacteria, yeasts, and other fungi through the influence of a change in environment. Most of these are, however, induced through changes in the medium under artificial conditions and they do not necessarily indicate a change in the direction of improvement of the organism or of greater complexity in its organization which may in turn point to the evolution of a higher form from a lower one.

Despite the foregoing, it is probably well to examine into certain facts with which we are familiar with regard to microorganisms, and which may, perhaps, have a close bearing upon what might be regarded as orthogenesis in bacteria. The first fact to which I wish to refer is that of parasitism. There can probably be very little doubt that parasitism on the part of bacterial cells is not an original, but an acquired character, using the term "acquired" in its literal, and not technical, sense. If that is granted, it would also follow that the acquirement of such a characteristic by a microorganism would mean the gradual adaptation of a bacterial cell from one kind of a medium to another. It would mean the gradual acquirement of partiality on the part of a microorganism towards certain chemical substances, certain temperatures, or certain other conditions which obtain only in a living host and not in an inanimate medium. The steps, gradual or rapid, by which the acquirement of such peculiar characteristics on the part of the microorganism would occur in its change from a saprophyte to a parasite would almost seem to imply evolution in a definite direction. In a sense, therefore, we may regard parasitism in bacteria as an evidence of orthogenetic development in such organism. It is, moreover, a case of evolution in a definite direction through the influences of environmental factors of the natural order and not those

which are produced artificially. In respect, therefore, of causal factors in the evolution of bacteria, we have parasitism exemplifying the antithesis, so to speak, of changes which we induce in bacteria in our artificial media, or by changes in the environment. These observations would seem to possess cogency, not only in the case of obligate parasitism, such as that characterizing the organism of human tuberculosis, or of anthrax, or of the fungus of wheat rust, but also that of what we may call facultative parasitism in which the organism may have adapted itself to life, both as a saprophyte and as a parasite through the influence of certain chemical or physical-chemical agencies in its environment which have rendered its protoplasm more highly adaptable than that of the obligate parasite. We may, therefore, regard facultative parasitism as an instance of orthogenetic evolution, just as we may so regard obligate parasitism. The puzzling question which may, however, arise, from these considerations is, which is the more advanced step in orthogenesis in parasitic bacteria. Is the obligate parasite the more advanced form, or is the facultative parasite the more advanced form? While many would probably, on first impulse, regard the former as the correct answer, it does not necessarily follow that such is the case. Certainly in this regard, a great many more facts are needed before any definite statements can be made.

Examples of other cases of orthogenetic evolution in bacteria other than the case of parasitism, which I have just discussed, may be multiplied *ad libitum*. But, owing to limitations of time and space, it will suffice to mention a few only.

The adaptation of bacteria to the physiological characteristic of nitrogen fixation, such as is possessed by all the *Azotobacter* species, and the *Clostridium* species and, to a slight extent, by many other species, can scarcely have been the result of anything else than a case of definitely directed evolution. This was probably accomplished through the influence of an environment in which

it was impossible for the organisms existing therein to live without acquiring a power of employing energy existent in carbonaceous material to fix atmospheric nitrogen and make it available for their own life processes. The next case which may be cited is that of the lactic-acid bacteria, which possess the power of transforming lactose (or milk sugar) into lactic acid. These cells are not in form or otherwise in function appreciably different from any other bacteria with which we are acquainted. They have, nevertheless, this specific and peculiar power to which I have alluded. Is it likely that they have acquired this power through any other influence than the influence of environment which operated in a definite direction and hence orthogenetically? The sulphur bacteria, or particularly those species of sulphur bacteria which have the power of oxidizing sulphur to sulphuric acid, are another case in point. The nitrifying bacteria are still another case in point. The iron oxidizing bacteria are still another case, and so we might go on and mention very many classes of bacteria, in each case of which there is a definite, distinct, and strikingly peculiar functional power which could not well have been developed without the influence of some environmental factor or factors operating in a definite direction. It is not so easy on the morphological side to give examples like those which I have just cited from the point of view of function of the bacteria. The reason for that has already been touched on above, namely, the simplicity of form and particularly the slight variety in form which characterizes the bacteria. In fact, it is my conviction that it is best to ignore, largely, morphological factors in bacteria when we study the problem of bacterial evolution. My conviction arises from a study of many and varied experiments which I can not discuss here.

Viewing our subject, then, from the standpoint that orthogenesis in bacteria would be concerned with progressive changes in the organism, principally physiological, due to its response to changes in environment, it

seems that we must admit that orthogenesis does exist there. But if, on the other hand, progressive changes like those in question must also be in the direction of producing a more advanced form of organism, we are confronted by a quandary resulting from a lack of an accepted definition for the term "advanced."

The argument that bacteria do not *at all* lend themselves to appraisal as regards evolution by the standards applying to the higher organisms is, perhaps, not sound as shown again by the researches of Löhnis, which I have just cited. The objection to viewing bacteria in a manner similar to the higher organisms because no sexual reproduction is known among them is removed by Löhnis' observations, which indicate that something akin to a real conjugation of cells does occur in the bacteria. His striking monograph in the Memoirs of the National Academy should be read and studied by all those who seek new light on the origin and nature of bacteria.

Another point of view which I believe may be introduced into this discussion with some justification results from a broad comparison of natural phenomena generally. In the inanimate world, we are confronted by the evolution of substances in series in which the first member of the series is simple and by small accretions becomes progressively more complex in the succeeding members of the series until very complex materials are finally built up. We are all well acquainted with the seriation showing progressive complexity in the hydrocarbons beginning with methane and going up; in the carbohydrates beginning with formaldehyde and going up; in the proteins beginning perhaps with amino acids and going up. Such examples of progressive seriation may be multiplied *ad libitum*. Why, therefore, should it not be possible that similar series should arise in the progressive evolution of bacteria through certain forces as yet largely unknown which cause accretions of characters, so to speak, to occur in bacteria through their being rendered more complex and complicated by the influence of

certain factors of the environment. It seems inconceivable to me that the great diversity and complexity of functional nature in the bacteria could have arisen otherwise. Nevertheless, analogies between phenomena in animate and inanimate nature must not be pushed too far in the absence of the necessary facts for their support. While I believe them to be of great significance, I do not desire to be dogmatic on the subject in the slightest degree.

While all the foregoing as regards the evidence for orthogenesis may be accepted as true, it does not follow that the doctrine of orthogenesis is anything new or significant or was so when it was first enunciated. It seems to me to constitute merely one way of describing the actual condition of progressive series in evolution, but it seems to me that it *explains* nothing. In so far, however, as its advocates espouse the cause of those who believe in and give evidence for the inheritance of acquired characteristics, the potency of environment in inducing fundamental and permanent changes in the organism, and the theory of mutation, they do contribute something significant to the discussions and experiments which constitute the amorphous symplasm, metaphorically speaking, from which our knowledge of the well-defined and real nature and origin of life may some day be expected to emerge.

It is, perhaps, of particular importance now to consider the bacteria as a class and their probable origin as bearing on the question for which we are trying to find an answer. There is a general disposition, and particularly is it true that there has been in the past, on the part of biologists and natural philosophers, so called, to place the bacteria in point of origin among the most primitive of living organisms. There is much inclination, indeed, to regard them as *the* most primitive organisms. While, superficially, this view seems attractive and correct, it loses much of its cogency when one takes into consideration the following situation: In all but a few

exceptional forms of bacteria, some of which I have named above, the physiological characteristic is either that of a saprophyte or of a parasite. It seems obvious to me that neither a saprophytic nor a parasitic organism can well be expected to originate in an environment which is devoid of elaborated organic matter. Subject to considerations which I shall discuss later, we must, therefore, accept one or two conclusions with regard to the origin of bacteria in the scale of evolution of organisms generally. Either they are the most primitive forms of organisms which have lost their primitive powers of living in purely inorganic media, or they are a much more advanced form of life which came to be after other organic forms had for some time been developing on the earth's surface. The first possibility is merely tantamount to saying that some cells of the most primitive forms have gradually adapted themselves to either a saprophytic or a parasitic existence and, therefore, is of little assistance to us. The correctness of the second conclusion, however, would seem to depend on many little-known factors. Still, it is the belief of many scholars. Putting the matter in another way for greater clarity and emphasis, I may state it as the opinion of several plant physiologists who have speculated upon this subject, that the primitive forms of living cells were probably those which could live in a purely inorganic medium. Obviously, such cells must have been limited to the group which we now call the autotrophic organisms, and of the autotrophic organisms, since the higher plants are certainly a very advanced form, we must have had something very much simpler, and the natural conclusion is that such a simpler form of organism must have been the single-celled green alga, or forms closely similar to it. If we assume that such was the case, then it is not difficult to propose a scheme of evolution of the bacteria which involves the gradual change of the unicellular green algæ into a variety of bacterial forms through the influences of environmental factors as I have already in-

dicated. It is not at all inconceivable that a green algal cell may have adapted itself gradually to life within a higher plant cell or within an animal cell, or to a saprophytic existence in soil or other media devoid of light. It may first have come there accidentally and then, through the power to respond to such an environment and to tolerate it, has gradually evolved new powers and has lost some of its old powers. It is conceivable, therefore, that whether we regard parasites and saprophytes among the bacteria as degraded forms or not, they may be examples of evolution in a definite direction, presumably in this case in the direction of greater complexity of function resulting from the urge of a constantly and markedly changing and potent environment.

Since the foregoing observations on orthogenesis in bacteria have led me to enunciate in another form a theory accounting for the origin of bacterial forms which has been discussed before, I feel constrained to go one step farther into that subject in order that my own views may not be misunderstood. While the idea of accounting for the origin of the bacterial cell from the single-cell alga seems attractive and appears to be in consonance with certain well-known facts, there are several troublesome features about it. In the first place, it assumes the development of so complicated and intricate a substance as chlorophyll before any form of living substance was evolved. While this may, of course, have been the case, it seems doubtful, in view of what we must consider to be the highly specialized nature of the green pigment of plants. In the second place, we have seen that the strong argument in favor of the theory of the single-celled alga as the primordial cell, or rather against the theory that bacteria may have been such primordial cells, lies in the well-known fact that most bacteria require organic compounds as energy for their life processes and that no organic matter could have been available without the activity of chlorophyllous organisms. This argument, however, overlooks two points, viz., first, the existence of

autotrophic bacteria and, second, the possibility and even probability that sufficient amounts of organic matter for bacterial purposes may have been elaborated at the dawn of life by chemical means, using the term "chemical" in the broadest sense. It is, of course, well known that the autotrophic bacteria, for example, the nitrifying bacteria, can live and build organic matter out of purely inorganic substances, carbon being obtained from carbon dioxide of the air, and in the absence of light and chlorophyll. But if this is so, why may it not be that of the known forms of living cells, the autotrophic bacteria were the first, since they are capable of living in a purely inorganic medium, the ammonia which is necessary to them being supplied from the small amounts resulting from chemical reactions induced by electrical phenomena in the atmosphere. As we have seen thus far, it may be argued, with equal justice, that the activity of the nitrifying bacteria is a highly specialized one on the one hand, and a very primitive one on the other.

But if, as just indicated, it should be argued that, after all, the autotrophic bacteria are exceptions in the bacterial world and that most bacteria need elaborated organic matter and hence they could not have been the primordial living cells, the second objection which I have stated may be urged, namely, that organic matter may have existed on the earth before living cells came into being. Mature reflection will render it highly plausible with the high temperatures, great electrical activity, and probable intense radioactivity which existed on the planet prior to the appearance of living cells, that unusual chemical activity inducing rapid and general combinations among the elements should have prevailed. This, moreover, involves the assumption of the existence of a degree of all these conditions which is requisite for the synthesis, but not for the rapid destruction of the organic matter, which must also be conceded as probable. Under such conditions, it is reasonable to suppose that bacteria, on being evolved as the primordial cells, may

have found the conditions requisite to their growth and further development.

It seems, on careful deliberation, that strong arguments may be brought forward for both the theory that single-celled green algæ and the theory that bacteria were the primordial organisms, if we consider merely the arguments which enter into the usual discussions of the subject. But it appears to me that we must penetrate beyond what is ordinarily called careful deliberation, if we would see other possibilities for explaining the origin of living matter. There is no logical reason for confining our attention in these discussions to the single-celled algæ and the bacteria which we know. There are, in addition, bacteria so small as to challenge and defy our ingenuity for devising means for rendering them visible. What may not further discoveries about their nature and requirements for life unearth for us which may be of the most vital significance to the solution of our problem? I have tried in imagination to go beyond, far beyond, the ultramicroscopic bacteria and have pictured to myself the following condition for the origin of living matter: A single molecule of organic matter, let us say, a polypeptid or a proteid molecule produced by the force which I have discussed, exerted as chemical energy, may, in floating about in its aqueous medium on the earth's surface, suddenly find itself in a field of radioactive force or some similar force which causes its atoms to orient themselves in such fashion and to vibrate in such a manner as to endow it with certain activities which we now regard as attributes of life. Crude though this conception may be, it constitutes a step, though perhaps a very bold one, into the realm of possibilities for explaining the origin of the first living cell, a subject which we must consider together with all our theories of evolution if we do not wish to remove the inspiration to progress by arriving at an impasse in our theories and our hypotheses.

In conclusion, it is well to review briefly the discussion which I have just presented in a very brief form. Out

of regard for your time and patience, I have merely presented in outline each of the important considerations which I deem of direct significance to the question at issue. I have presented the difficulties which lie in the path of treating bacteria from the point of view of orthogenesis, and yet have shown that they may be so treated with certain justifiable assumptions as a basis. Having thus treated them, however, I have shown that whether the theory of orthogenesis holds for bacteria or not, it can not be considered as explaining anything, but merely as a mode of describing our observations. I have gone into the more fascinating and what seems to me to be the more useful discussion of the origins of living cells and the position of the bacteria with regard to such primordial cells. I have mentioned the various hypotheses which, in my opinion, may be considered to be the most plausible in that connection, and have shown the weaknesses and the strength of each. It has been my purpose to give an unbiased presentation of my own hypotheses and those of others without prejudice to any so that you might be enabled to discuss them all and arrive at your own conclusions. Without a thorough review of the literature of bacterial physiology and morphology, it is not easy to obtain a broad enough view of the subject to do it justice and I would urge particularly that those who are interested in it acquaint themselves with the absorbing and inspiring literature of the subject of mutation in microorganisms. I believe that it is full of significance for biological progress and I wish that circumstances made it possible for me to present a brief review of it for your consideration. As it is, I must content myself with directing your attention to it and with expressing the hope that my humble efforts in preparing and presenting this paper will constitute a step forward in our progress of thought and experimentation on problems in the evolution of living matter.

ORTHOGENESIS AND SEROLOGICAL PHENOMENA

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As my discussion progresses I fear that some of my hearers may be reminded of the old joke about the mongoose. A stranger carrying an odd-looking box was asked by a man whose curiosity got the better of his good manners, what was in the box. The stranger replied that it was a mongoose and went on to explain that his brother was subject to delirium tremens, during the attacks of which he believed that he was being strangled by snakes; this mongoose was to catch the snakes. To the reminder by the inquisitive man that these were imaginary snakes he retorted, "Yes, I know, but this is an imaginary mongoose."

Since some of our most competent investigators in the fields of genetics and evolution are skeptical apparently about the whole question of orthogenesis, to them, at least, I shall be making an imaginary attack upon a mythical phenomenon. President Kofoed, however, seemed to think that some of the recent work with immune sera done in my laboratory, which strongly indicates the induction of permanent germinal modifications, might have possible theoretical implications bearing on the question of orthogenesis, and I agreed to discuss the subject, although realizing at the outset that the net result would not be a scientific proof, but merely a suggestion which might possibly be of some value as one of various working hypotheses.

First as to orthogenesis itself; is there such a process? Our answer must depend largely upon how we define orthogenesis. It takes but a glance at the literature of the subject to see that it has meant many different things to many different people, ranging from a mystical inner

perfecting principle, to merely a general trend in development due to the natural constitutional restrictions of the germinal materials, or to the physical limitations imposed by a narrow environment. In most modern statements of the theory, the idea of continuous and progressive change in one or more characters, due according to some to internal factors, according to others to external causes—evolution in a "straight line"—seems to be the central idea. To many, faced by the seeming impossibility of explaining by natural selection the origins of new characters, it has been apparently merely a welcome general utility concept by which one may account for the beginnings of new organs, or the development of parts along definite lines, irrespective of utility.

For present purposes nothing is to be gained by a review of the different theories of orthogenesis, all so well summarized in Kellogg's "Darwinism To-day," and I shall proceed merely on the assumption that, judging from the statistical law of errors, certain variations are apparently not fortuitous, since they tend to accumulate in certain directions. It is customary to add that the lines of development which result are independent of, and in extreme cases may be opposed to, the operation of natural selection. I see no reason, however, for believing that if variations occur in definite directions of no use to the organism, why they may not also occur just as definitely in directions which lend themselves to the perfecting influences of natural selection. The difficulty in determining this point lies in the fact that an evolution based on the selection of even fortuitous variations must in one sense be orthogenetic, that is, along definite lines, so that there is no way in retrospect of telling whether the underlying germinal variations were purely fortuitous, or whether they were biased toward an adaptive outcome.

Of the various lines of evidence brought forward in support of theories of orthogenesis, the ones which appeal most convincingly to me are: (1) those based on

parallelisms in variation which appear in different branches of the same large group of organisms; (2) those argued from the premise that the very nature of the chemical complexes which constitute the body of a living organism necessarily limit changes to relatively few directions; and (3) some of those instanced in the field of palæontology.

As to examples of parallelisms in related forms, I am most familiar with conditions to be seen in the color patterns of the pheasants (*Phasianinæ*) and the guineas (*Numidinæ*). In a paper¹ written some years ago I summarized my observation on various features of the coloration in a number of groups of genera and species in these two subfamilies as follows:

... there are certain basic tendencies for particular elements of the coloration, such as the formation of eye-spots, barring, and the like, to follow along definite paths of development. When arranged with reference to one of these elements, such, for example, as barring, which is one of the most universal, instead of possessing distinct and unrelated markings, the different species in a given group are seen to be standing merely at different levels in the development of one, or at most a few, continuous progressions of the special pattern in question. Since when so grouped the gradation in pattern is as much in evidence between collateral kinsmen as between those of direct lineage, one can only conclude that the bias toward a particular line of patterns is the product of fundamental protoplasmic peculiarities implanted in the group as a whole.

Further on in the same paper it is shown that where the pattern has become obscured it may be brought to expression again through hybridization. In the interesting group known as the peacock pheasants (*Polyplectron*) which by systematists is regarded as intermediate between the peafowls and the pheasants in the narrower sense, the varying stages and types of ocellation to be seen afford a good illustration of the point at issue. Quoting again from this earlier study:

Again as regards ocelli or "eye-spots" in *P. chalcurus*, which appears to be the most generalized species, one finds no ocellation. The only hint of what is to be realized in the more specialized

¹ *Jour. Exp. Zool.*, VII, 4, 1909.

members of the group is found in a pronounced purplish and greenish "metallic" coloration present on certain feathers of the tail. In the male of *P. emphanes*, while there are numerous green metallic iridescent areas on the feathers of the upper wings and back, they have not yet progressed to the condition of being definite ocelli, although on the tail of this same individual there are two transverse bands (the one on the retrices, the other on the upper tail coverts) of ocelli. Still a step in advance, in the male of *P. thibet-anum*, Gm. (*P. alboocellatum* Cuv.; type, Mus. d'hist. nat., Paris) the small feathers of the wings and the feathers of the inter-scapular region bear distinct small purple ocelli ringed successively with black, light brown, and white. The tail is also banded with ocelli. In the male of *P. germaini* the wing-coverts and back bear numerous green ocelli. The female of this species, as usual less advanced phylogenetically than the male, has the ocelli of the body much less distinctly marked.

An idea frequently attached to the theory of orthogenesis, yet which I believe is in no wise a necessary part of it, is that the various grades of a feature supposed to show orthogenesis have arisen as a connected succession, the supposedly most advanced stage having emerged from the stage next in order below it. That the individuals of a large group which show some particular characteristic expressed in different degree can be arranged in a gradational series with reference to that characteristic is obvious, but, as pointed out by various critics of the theory, this does not prove that the various expressions of the character in question arose thus sequentially. In a recent study yet unpublished, made by Miss Sarah V. Jones in the department of genetics at the University of Wisconsin, on the genetical behavior of checks and bars in inheritance in pigeons, for example, Miss Jones corroborates the results obtained by Staples-Browne and by Bonhote and Smalley which show that the two patterns are independently inherited in Mendelian fashion with checked-wing dominant to barred. She also found the relation of uniform black to check to be one of simple dominance, and furthermore, that certain grades of checking are inherited independently. But she found no evidence in support of the well-known view of Whitman that

the various grades of checks form a series moving in one direction, the ultimate outcome of which is the two-barred and finally barless types. And Miss Jones points out that it does not "necessarily follow that because the interaction of these several factors produces an apparent epistatic series, the mutations producing the various grades of checking should have occurred in any particular order."

And here, to my mind, is the crux of the matter. In order to have what may legitimately be termed orthogenesis, do the underlying mutations have to occur in any particular order? Is not the very fact that, instead of existing as a medley of wholly unrelated elements, certain characteristics of organisms, such as color markings, can frequently be arranged as parts of a definite pattern or as stages in a general process—does not this in itself indicate directional variation? When one sees in its incipency, as it were, in one species a character which has attained to an advanced expression in a kindred group, especially where there are intermediate expressions of the same characteristic in other related species, is not this indicative of a general trend in variation? For instance, is not the tendency toward the formation of "eye-spots" in the plumage of the pheasants hinted at even in the greenish-black iridescence so often visible in the tail feathers of the common rooster—is not this tendency the expression of what in last analysis must be a germinal bias? To be sure, this bias finds different ranges of expression in different species: as eye-spots on the wing-feathers in some species, on the body-feathers in others. In one species they may occur as a single row of ocelli, in another as two rows, across the tail. And it is obvious that certain of these patterns have not been derived directly from others, since they appear in what are clearly collateral lines. Nevertheless, the tendency to form ocellations is present in many if not all species of this great group. We know nothing of the order in which the mutations occurred which brought about any partic-

ular condition that at present exists in the group. Some of them may have been small and sequentially related, and it is not impossible that the extremes were thrown in one line, while grades of less advanced type came into expression in collateral lines. It is also clear that even should certain grades have arisen as a progressive series there is no reason, from the viewpoint of the mutation theory, why any two particular grades should not show the characteristics of Mendelian unit-characters, irrespective of the order of their origin. The important point is that in this group when mutations occur in certain color pattern-controlling factors, whether great or small, they tend toward the formation of eye-spots in some degree.

While we know little of the chemistry of animal pigments, the reactions involved in color-production in certain plants are better understood, since many of the pigments have been extracted and analyzed. Along with the understanding of structure that has been gained in the chemical studies of synthetic dye-stuffs, has come considerable knowledge of the relation between color and molecular structure. In many cases, for instance, as Nietzki² has shown, where the pigments of most simple construction are yellow, by increase of molecular weight they change to red, next to violet, then to blue. A good review of the theories of color in organic compounds, given as an introduction to her own painstaking and valuable chemical researches² on "Pigments of Flowering Plants," will be found in a recent paper by Dr. Nellie A. Wakeman. Most of the information about organic pigments used in the present discussion has been obtained from this source.

Upon reading such a piece of investigation together with the accompanying discussion of related studies one is impressed by the fact that a comparatively few processes underlie most pigmentary changes in plants. Enzymes—hydrolases, reductases and oxidases—frequently

² *Trans. Wis. Acad.*, XIX, Part II, pp. 767-906, Madison, Wis.

play an important part in the formation of pigments, or in changes in pigments already formed. Shade of color, for example, is evidently often merely a function of oxidase content. With a graded increase of oxidase, therefore, a plant might be put through a regular gamut of color effects. In general, the mere addition of hydrogen to dye-stuffs reduces them to the corresponding leuco base. Armstrong, in his quinone theory of color, makes much of the quinones as the colored compounds in dye-stuffs and maintains that the corresponding colorless compounds are hydro-quinones. The structure and size of the pigment molecule itself seems to be an important factor in color. Hydrocarbon radicals, for instance, deepen the tint; the addition of hydrogen raises the tint. In analyzing any particular case one has to take into account the original molecule, the position of any group introduced and the number of groups introduced. It is possible, for example, by the introduction of a tint-deepening group to deepen the color, but by introducing two or three more such groups to throw the absorption wholly outside the visible spectrum and thus do away with the color. From this it is clear that two compounds may be closely related in constitution and yet one be colored, the other colorless. As to why, physically, in both the aromatic and the aliphatic series, color is produced in certain compounds and not in others, various investigators have arrived at the conclusion that the cause of color is due to "the making and breaking of contact between atoms, thus giving them marked activity," a process known as *isorropesis*, and Miss Wakeman goes on to explain:

This change of linkage which must accompany the transformation of one modification of the compound to the other is the source of the oscillations producing the absorption bands. If these oscillations are synchronous with light waves of a high frequency they give rise to absorption bands in the ultra violet and the compound is colorless. If, however, they are less frequent, the absorption band appears in the visible portion of the spectrum and this absorption of colored rays results in the compound taking on complementary color.

Among interesting facts that come to light in Miss Wakeman's summarization may be mentioned the following: all organic pigment molecules are unsaturated; the quinone grouping is one of the best known of the chromophorous groups; by far the largest number of plant pigments are referable to hydrocarbons of saturation C_nH_{2n-14} and C_nH_{2n-16} ; and finally, that it is the relation of the chromophorous groups to each other and to the rest of the molecule, and not their mere presence in the molecule, that postulates color in a substance.

I may seem to have dwelt unduly upon pigmentation in plants but I have tried to go into the matter only sufficiently to give a glimpse of some of the real conditions which underlie some of the "unit-characters" we are juggling about in genetics, and around which we are attempting to frame hypotheses of evolution. Color, perhaps more than any other one thing, has in recent years been utilized for genetical observations. And when it is known that in many cases color is merely a function of the degree of oxidation of some fundamental compound, or the introduction or subtraction of some hydrocarbon radical, it does not tax the imagination to conceive of how it is possible to have series of color "characters" that in the parlance of organic evolution represent orthogenetic series. As simple a matter as the relative degree of oxygen supply, probably determined by the amount of an oxidase present, may account for various stages of color. It is manifest, moreover, that in a given group there might easily be a tendency toward increase in oxidase-production, which if present unequally in different collateral lines might give us just the uneven condition, with different species standing at different levels of expression of the trait in question, which exists in various alleged cases of orthogenesis. It is obvious, furthermore, that any higher state of development of the character in a particular species need not have sprung from the next lower stage, but may have had its immediate origin from any level of the scale.

Most of the constitutional changes which go on in the living organism seem to center in the proteins of the protoplasm. Metabolism is largely a question of the disruption and reconstruction of the various cell-proteins. In the cell, moreover, the characteristic protein-complexes themselves determine the nature of the synthesis that shall go on. When synthetic activity is more than sufficient to make good metabolic waste, growth results, and when such increase becomes overgrowth and takes the form of a detached individual, we pronounce it reproduction. We are then in position to talk about inheritance—the fact that a new individual possesses the properties and, under similar conditions, therefore, will express the activities and take on the appearances of the earlier or parent form. Thus the germ-cell is a reduplication of the zygote from which it sprang, a detached bit of living matter made up largely of certain characteristic protein-complexes. Even the simplest protein is a huge molecule built up of a series of different kinds of amino-acid “nuclei” which in different proteins differ in numbers, kinds and arrangements. Certain of them seem necessary to all proteins, others are present in only some proteins. Each amino-acid, besides being linked to its fellow, has a replaceable hydrogen atom which may be exchanged for any one of several radicals or “side-chains.” Furthermore, the ordinary native proteins are secondarily compounded of a number of the simpler blocks formed of linked amino-acids. The unitary amino-acids which enter the blood as protein digestion-products are used as building units again, each cell selecting the kind of units it requires for replacements in its own proteins.

We have no reason to believe that the proteins of the germ-cells have any mysterious powers associated with them that are not shared by any or all of the somatic cells. The modern view of embryogenesis and histogenesis no longer finds it necessary to picture troops of pangenes departing from their home in the nucleus at just the proper time to take possession of the cytoplasm

and turn the cell into a specific tissue-cell. Each tissue-cell probably retains all the essential properties of the original fertilized ovum from which it has directly descended. In many cases, among lower organisms, at least, we know that somatic cells detached as buds or experimentally can through regulation and new growth reconstruct themselves into complete organisms. That a particular cell takes on the characteristics of a specific tissue seems to be determined by the special environment in which the cells happen to be placed in the organism.³

Exactly how much chemical difference there is between two unlike tissues or between the cells of a particular tissue and the germ-cells is not known. As far as we have any cytological evidence to the contrary the nuclei, at least, of the tissue-cells are not essentially different from the nuclei of the germ-cells. While the various tissues differ very much in appearance, this is mainly the result of the accumulations of intercellular products or of cytoplasmic modifications. And many of the latter may be largely changes in colloidal state rather than fundamental changes in chemical composition. In any event, the new condition is one which has sprung from a cellular chemical constitution similar to that of the original zygote. And if this is true, would not any internal or external agent which could affect particular proteins of the somatic cells be able also to influence the homologous elements in the germ-cells?

Inasmuch as I have already twice reported to this Society on the work⁴ of Dr. Smith and myself with fowl-serum immunized to rabbit-lens by means of which, through injections into pregnant rabbits, we succeeded in obtaining defective-eyed young, I shall not again relate the details. The most interesting thing about the experiment was the fact that the eye-defects were transmissible to subsequent generations, and inasmuch as the condition

³ Cf. Child, "Individuality in Organisms"; also "Origin and Development of the Nervous System."

⁴ *Jour. Exp. Zool.*, 31, 2, 1920. *AM. NAT.*, LV, 1921.

could be passed down through the male line alone it is evident that it is based on changes in the germ-cells.

In later experiments we obtained similarly defective young by injecting rabbit-lens into pregnant rabbits, although we secured this result only after repeated trials and in the young of but one female. Our belief is that the cytolytic serum not only attacked the newly forming fetal lens, but also its representatives in some of the germ-cells of the fetus. This implies, of course, that there is a sufficient thread of chemical identity between the two to render them both susceptible to the same specific influence.

For such serumal effects to be of significance in evolution, however, the antibody or other factor operative on a given tissue-protein would have to be one that could arise directly in the organism itself. But since it is known that animals will develop anaphylaxis against tissues of their own species, and that a rabbit can be made to build spermatotoxins against its own spermatozoa, it is reasonable to suppose that if an animal's own tissues became displaced, injured or otherwise modified, they might cause the production of antibodies. And these, carried by the circulating fluids of the body into the gonads, would have opportunity to influence such protein-complexes there as were similar to those in the tissues which served as antigens. Nor need the germinal and somatic elements in question be identical in constitution, for it is known that while an antibody against a particular tissue shows its highest degree of specificity only against that tissue, nevertheless, it will also react in some degree with other tissues of the same individual. This phenomenon, termed species-specificity, clearly indicates that there is a broad common basis of chemical identity underlying all the tissues of an organism. It is not unreasonable, then, to believe that there is sufficient chemical identity between the proteins of tissue cells and the related proteins of the germ for both to be influenced by the same agents.

To construct a working hypothesis upon the possibilities

before us we might suppose that as long as all tissues are in normal physiological balance no antibody or similar modifying agents are developed. The germ-cells, therefore, maintain the exact constitution they derived from the zygote from which they descended. But with the occurrence of injury, undue stimulation or pronounced change in any part of the body, serological changes would probably be produced in the blood-stream and the germ-cells would then be exposed to possible modifying influences. This would be more likely to happen, of course, if the exposure continued through a long period of time. If the influence were disintegrative or poisonous as the cytolytins or cytotoxins evidently are, then probably degenerative changes would ensue. Such a hypothesis affords, perhaps, a plausible explanation of such deteriorative evolutionary processes as those seen in the formation of vestigial organs. As a concrete illustration, purely hypothetical of course, we may suppose that such a species as the mole in gradually changing to a subterranean existence would meet with frequent injuries to the eyes, and that, as a result of the ensuing inflammatory and suppurative conditions, resorptive influences would be set to work which not only affected the proteins of the eye, but also the related proteins of the germ. Once the degenerative process got to going, it might for a time be based in each new generation upon both the direct chronic irritation to the eye and the parallel changes induced in the germ. Finally, we may suppose that the somatic influence would cease when the eyes became of small size and the eyelids remained permanently sealed, but that the conditions induced in the germ would persist. If such atrophied eyes continued to be resorbed more or less in each generation, however, variation toward still further reduction might continue in the germ. Such a progressive degeneration might possibly be ranked as an instance of regressive orthogenesis.

But what of the progressive aspects of evolution? Can serological reactions be invoked here with any show of reason? One great difficulty in dealing with progressive

variation is that we know almost nothing about the chemical and physical factors which underly growth, hypertrophy, hyperplasia, metaplasia, or other changes in somatic tissues due to changed internal relations or to unusual environmental stimuli. If we only knew, for instance, what happens in even as simple a case as when epidermal cells develop into a callous in response to undue pressure or friction, we might have a clue as to how, also, constructive changes might occur in germ-cells; but we have no such knowledge.

Certain types of tissue-overgrowth⁵ in which there is increase in the size of the tissue-elements (*hypertrophy*) or in the number of such elements (*hyperplasia*) are interesting in this connection. For example, increased strain in bone leads to increased growth of bony tissue, or excessive exercise leads to overdevelopment of certain muscles. In such cases an increased demand on the nutritive stream caused by unusual katabolism results in a physiological hypertrophy. That is, an excessive synthesis of certain types of proteins is set up. Does the impetus to such extra synthesis extend also to the related, though unstimulated, tissues? I know of no evidence bearing directly on this point, although such phenomena as compensatory overgrowth show that there are influences at work outside the immediate tissue itself which are instrumental in inducing the hypertrophy. For example, if one of a pair of organs (lung, kidney, testicle, thyroid) is lacking or is destroyed, the other enlarges in a short time to the size and functional capacity of the pair combined. There is considerable evidence, particularly in the field of pathology, to show that under ordinary conditions the tissue-elements exert a sort of balanced reciprocal restraint, but disturb this and the whole system is more or less deranged until a new equilibrium is established. Since in compensatory adjustments the compensating organ is generally not in direct connection with the one which is missing or disturbed, it seems probable that the agent which incites the hyper-

⁵ Cf. any General Pathology.

trophy is carried by the blood, although the possible influence of the nervous system must also be reckoned with in higher animals. And if there is such a serum-borne agent in the case of compensatory hypertrophy, may there not also be one in that of the ordinary physiological hypertrophy of the exercised muscle or stressed bone? If so, we must keep our minds open to the possibility that it may also stimulate the germinal prototypes of such proteins to additive functioning. For if we had but a single side-chain in common between a protein of somatic tissue and a protein of the germ, anything that could affect one might well be expected to affect the other.

Again, mechanical stimuli, if not too severe, and various irritative substances in amounts sufficiently small not to be destructive or poisonous to the tissues, may stimulate cells to overgrowth. Very small amounts of arsenic or phosphorus, for example, may thus affect the kidneys and liver, and minute doses of phosphorus may cause increased growth of bone. In such cases also it is probable that serological changes are involved. This is almost certainly true in cases of vicarious overgrowth, where an organ supposedly of related function takes over wholly or in part the work of another tissue. An example of this is seen in the enlargement of the pituitary gland when the thyroid is atrophied or removed, or the compensatory enlargement of the hemolymph glands and bone-marrow following removal of the spleen. Still further may be cited the phenomena of metaplasia, in which, through modification of function and nutrition, specialized tissues develop from cells which normally produce tissue of another order. It sometimes happens, for example, that the choroid coat of a severely injured eye, after the lapse of considerable period of time, will develop a layer of true bone. In fact, metaplastic formation of bone is common in many tissues. Such facts show that many, if not all, tissue-cells have the capacity to form very different kinds of tissue in different environments, and suggest that they retain all the inheren-

cies of the germ. They are what they are somatically because of the special restrictions or excitations of their particular situation in the organism. But if these highly specialized tissue-cells can be so stimulated as to form an entirely different type of tissue, may not such stimulative influences invade even the germ-cell with modifying effects?

Lastly, there are the endocrinal secretions to be reckoned with. Since they are at present popular subjects of research and are constantly being alluded to and discussed in the biological literature of the day, I need not review the field. It is evident that in them we have circulating through the body a series of powerful substances capable of producing profound effects in any or all parts of the body. Through them, apparently, various organs effect reciprocal stimulations and the tissue-complexes of the entire body are maintained in a state of general physiological equilibrium. Both clinical and experimental evidence reveals that hypertrophy or atrophy of an endocrine gland may be followed by marked alterations of structure or function in one or more regions of the body. Thus the cretinism or the myxœdematous condition which results from removal of the thyroid or arrest in its function, or the symptoms resembling exophthalmic goiter following hyperthyroidism are familiar examples. The remarkable overgrowth of the bones of the extremities and head known as acromegaly—morbid giantism—associated with enlargement of the pituitary body is another. Also the relations of the gonads to the secondary sexual characters are well known, as is that of the fetus to the normal hypertrophy of the mammary glands in pregnancy.

Since hypertrophy or atrophy of an endocrine may produce deep-seated permanent changes in various tissues of an organism, I would again point out the possibility that the germinal homologues of the proteins of such tissues, if such there be, might likewise be permanently modified, and that if for some reason there came a constant inherited increase or diminution of an endocrine

gland, or an environmental modification of it generation after generation, we might have in its waxing or waning output the excitant necessary for germinal changes which become outwardly expressed as a series of orthogenetic changes. That this suggestion of endocrinal influence on the germ is not so far fetched as would appear at first sight, is evident, I think, when we recall that certain of the conditions which can be induced in individuals by experimental or pathological endocrinal upsets are known to occur also as congenital defects which are inheritable. For example, short-fingeredness (brachydactyly) may be induced after birth by too much pituitary secretion, but such a condition is also well known as a congenital defect which is hereditary. In the latter case, is it more reasonable to suppose that the short-fingeredness, could we trace it back into the germ, is really represented by a factor that has to do primarily with the finger or with a factor directly concerned in some way with the pituitary body? And did hypertrophy of the pituitary body originally induce the heritable type of brachydactyly? We do not know, but the parallelism of the two conditions, it seems to me is highly suggestive.

And let us glance for a minute at one of the well-known studies on orthogenesis; that of Ruthven⁶ on the variations of scutellation in the garter snakes. In his own words:

... it seems to me that the most tenable hypothesis of the evolution of the genus *Thamnophis* is that it originated and became differentiated into four main groups in northern Mexico. From this region the groups radiated in all directions, but principally to the northward, and wherever they entered different regions the changed environmental conditions acted as an unfavorable stimulus which retarded growth, and differentiated the groups into dwarfed forms.

And in another place he generalizes as follows:

(1) That the maximum scutellation and size in the genus *Thamnophis* occurs in the center of dispersal, and the forms that have been produced in the history of its migration have been formed principally by dwarfing and by a reduction in scutellation; (2) that the variation in the number of scales in the different series is

⁶ Bull. 61, U. S. Nat. Mus., 1908.

definite and not promiscuous, and is correlated in a remarkable degree with changes in the environment.

Have we not here a condition strikingly like what we should expect to find if some factor or factors, external or internal, were operating in such a way as to lessen the output of some endocrinal secretion concerned in growth or the determination of size? This is at least a possibility worthy of consideration.

In closing may I say that in what I have put before you I do not pretend to have supplied the established facts necessary for founding a scientific theory. The discussion is largely a series of suggestions, a mere working scheme which takes into account various phenomena that appear to be related, and which in their present states of disclosure seem to lend themselves to some such interpretation as I have tried to give. It is presented because, in my estimation, it suggests a line of thought we may well entertain when we are wrestling with our several problems of genetics, variation and evolution. For if it can be clearly established that any one of the serological influences can reach specifically from soma to germ then it becomes a plausible hypothesis that many of them do. If a changed or changing external or internal environment causes a long continued physiological stress of certain parts, then as long as this stress is accompanied by changed conditions of the circulating fluids of the body, so long also will the germ-cells be exposed to these influences. If they are such as to induce variations in definite directions, orthogenesis must be the outcome.

And if serological influences play an important part in adaptive somatic changes, such as adaptive hypertrophies—or for that matter, adaptive atrophies—then we have the way open to conceive of how adaptive germinal changes may likewise be the outcome of these same influences.

It is a noteworthy fact that in the geological past whenever conditions suitable for new types of existence occurred, new forms of life well adapted to the conditions appeared. This has happened not only once, but

repeatedly. And since satisfactory adjustment to the new conditions must mean not only one, but many favorable and interrelated variations, it seems almost incredible that the adaptedness characteristic of the organisms in question was attained merely through the operation of natural selection generation after generation on assemblages of purely accidental mutations. Palæontologists tell us that times of marked evolutionary change have coincided with periods of great geological change—extremes of temperature, moisture or drought, or fairly rapid fluctuation between such extremes. And while such conditions would undoubtedly favor a maximal operation of natural selection, it is well to remember also that the severe strains of somatic adjustment forced upon organisms existing at the time would doubtless result in a maximal sweep of serological influences through the sorely pressed body.

Although I have emphasized one side of the problem of variation, I am not unmindful of the remarkable stability of the germinal protoplasm as we see it expressed in organisms to-day. It is obvious that not every minor or temporary alteration in somatic mechanism is reflected in the germ to any measurable extent. Since probably no two living things of any kind are equally susceptible to external influence, individual germ-cells doubtless vary in susceptibility, possibly even the same germ-cell would respond differently at different stages of maturity. It is not unreasonable to believe, moreover, that only a few out of many germ-cells might be sufficiently affected to make a perceptible difference. I have already expressed the opinion⁷ elsewhere that “no one to-day, qualified by his knowledge of embryology and genetics to the right of an opinion, would, I think, deny that the new organism is in the main the expression of what was in the germ-line, rather than of what it got directly from the body” But we know that the germ does change from time to time and it seems to my mind not illogical to suppose that at least some of the changes are specifically related to changes in the soma.

⁷ AM. NAT., LV, Mar.-Apr., 1921.

ORTHOGENESIS AS OBSERVED FROM PALE-
ONTOLOGICAL EVIDENCE BEGINNING IN
THE YEAR 1889¹

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1. THE ORIGIN OF SPECIES

THE Origin of Species is now clearly understood in the hard parts of invertebrates and of vertebrates, and there is little to be added as to the *modes of mechanical evolution*. No chances or experiments are tried by Nature. The process is continuous, adaptive, mechanically perfect in every Mutation of Waagen. As shown in actual observations by all close students of vertebrate and invertebrate morphology during the last fifty-two years, and as summed up in the remarkable contribution of D'Arcy Wentworth Thompson (1917) on "Growth and Form," animal mechanisms compete with each other in close analogy to humanly made machines—automobiles, typewriters, aeroplanes. Consequently, while Nature is constantly standardizing her machines through individual competition and producing flocks of birds and shoals of fishes which are so precisely alike that animals of the same age, sex, environment and heredity *show no perceptible variation*, she is also frequently substituting more perfect and more adaptable machines and discarding older and less adaptable ones, exactly as man is doing in the case of his automobiles, his typewriters, and his aeroplanes. Thus the naturalist and the paleontologist

¹ Illustrated by twelve lantern slides exhibiting mutations of *Ammonites*, of *Spirifer*, of *Paludina*; rectigradations of the grinding teeth of lemuroid Primates; evolution of proportion from the rhynchocephalian type of *Hatteria* to the dinosaurs and birds of the genera *Deinodon*, *Struthiomimus*, and *Diatryma*.

ist are alike impressed with the incessant action of Natural Selection on animal mechanisms and with the new testimonials to this aspect of Darwin's great principle.

When it comes to the *origins* either of new characters or of new proportions quite different is the attitude of observers of mechanical evolution; no evidence whatever has been forthcoming from the same fifty-two years of close observation and research as to the *causes* of origin, at the same time the *modes* of origin of all mechanical characters are indubitably orthogenetic.

To further clarify the bearing of palæontology on orthogenesis, I desire to point out that all visible mechanical evolution goes hand in hand with invisible physicochemical evolution; and that there are steps in evolution which are primarily physical, others which are primarily chemical, others which are primarily mechanical. Therefore the experimental botanist, zoologist, biochemist, biophysicist, or geneticist, has the opportunity to win immortal fame by discovering the causes of mechanical evolution.

Meanwhile the palæontologist enjoys the entirely unique position of being the only competent observer of the Origin of Species so far as specific characters are recorded in the hard parts of animals and the relatively few soft parts which are preserved in a fossil condition.

2. ORTHOGENETIC ORIGIN OF NEW CHARACTERS

All agree that sound induction either as to the origin of new characters or their transformation is an exceedingly difficult matter. It has taken me thirty-three years of uninterrupted observation in many groups of mammals and reptiles to reach the conclusion that the origin of new characters is invariably orthogenetic.

In 1889 I first observed (Osborn, 1889.46) that new cusps originate on the grinding teeth of Eocene Primates, now recognized as lemuroids, in a definite and adaptive manner from minute shadowy beginnings which are mechanically adjusted to similar minute shadowy

beginnings of opposing cusps in the other jaw; whereby there evolves a continuous reciprocal mechanism not dissimilar to the reciprocal services of the Yale key and the Yale lock. The evolution of the key below proceeds with the evolution of the lock above. The process does not go very far in the Primates, but in the purely herbivorous ungulates, like the horse and the elephant, the reciprocal grinding mechanism reaches a degree of complexity to which the most intricate lock and key devised by man present but a feeble parallel. Every mechanical device in the upper grinding teeth, adapted to the fine comminution of grasses, is *reversed* in the lower grinding teeth, on the principle of mechanical action and reaction; nowhere in nature is reciprocal mechanical co-adaptation more perfectly evolved than in the upper and lower grinding teeth of mammals.

Between 1889 (Osborn, 1890.47) and 1891 (Osborn, 1891.53) I made what I now believe to be an *unsound induction* from this evidence that this continuous mechanical origin tended to support the Lamarckian theory of the inheritance of adaptive reactions. I first termed the orthogenetic process "definite variation"; later I termed it "progressively adaptive variation"; by the year 1908 I realized that these new adaptively arising tooth elements were not variations in Darwin's sense at all, and I applied to them the distinctive term *rectigradations* (Osborn, 1908.314). In the meantime I abandoned the Lamarckian explanation and in 1895 (Osborn, 1895.97) I started out upon a *search for the unknown factors of evolution*, a search in which I am still busily occupied.

To return to the difficulty of making sound inductions as to the origin of new characters in hard parts, in 1889 I opened a long correspondence with the leading exponent of Darwinism in Great Britain, Edward B. Poulton, who admitted the evidence but interpreted the facts in the Darwinian way, namely, as the selection of mechanical successes from non-observed mechanical failures. It is a good thing to have a number of skeptical friends

about; it sharpens your powers of observation and makes you much more cautious about your inductions. My original observations on the Primates required corroboration, and this I have sought through the observation of the origin of new characters in many other kinds of mammals traced in their evolution over very long periods of time, especially the horses, the rhinoceroses, and recently the proboscideans, but most profoundly and exhaustively the titanotheres, an extinct family remotely related to the horses, which I have studied monographically for twenty-one years.¹

Even by trying to keep an absolutely open eye and mind, entirely uninfluenced by any theory, or preconception, or opinion, I have been unable to find a single exception among these many different kinds of mammals to the observations made on the Primates in 1888 and 1889; not a single new organ is observed to arise fortuitously or indefinitely; it always arises gradually, continuously, and adaptively from its minute shadowy beginnings. This continuous reciprocal, mechanical co-adaptation seems to be an established fact in evolution, and is established most strongly where explanation or search for causes seems to be most difficult.

I am not enthusiastic about the adoption of the term orthogenesis, admirably significant as it is in its Greek derivation, first, because Eimer connected it with Lamarck's and Buffon's principles of inheritance of acquired modifications, and, second, because it does injustice to the first great observer of direct adaptive origins in nature, namely, the German palæontologist Wilhelm Heinrich Waagen, whose observations in 1869 laid the foundation of all subsequent work both among the in-

¹ Osborn, H. F., "The Titanotheres of Ancient Wyoming, Dakota, and Nebraska. Life and Geography of the Central Rocky Mountain Region in Eocene and Oligocene Times. Evolution of the Titanothere Family. The Causes of Development and Extinction of Mammals," *U. S. Geol. Survey Monograph No. 55*. [Unpublished.] Completed for the Survey June 30, 1920. This monograph is the most complete and exhaustive analysis that has thus far been made of the evolution of any family of organisms.

vertebrates and the vertebrates. To the best of my knowledge he was the first naturalist to observe how new species actually arise in nature. Compare Waagen's description (1869) of the genesis of new characters in the shells of cephalopods (*Ammonites subradiatus*) with those which Osborn (1889-1921) has observed in the teeth:

"Thus the species if considered as such may be conceived and considered as a species, but in contrast with earlier or later forms [i.e., ancestors or descendants] as a mutation. Now as regards the value of these above-defined conceptions, variety and mutation, on closer consideration a quite decided difference in value becomes apparent. The former conception [variety], in the highest degree variable, appears to be of small systematic value; while the latter [mutation], although in minute characters, is highly constant, always surely recognizable; on which account far greater weight must be put upon Mutations, they ought to be very precisely denoted and held fast to with great persistence."

Twenty years later the German palæontologist Melchior Neumayr observed this process of continuous development, generation after generation, in a certain definite direction for which he proposed the term "*Mutationsrichtung*." Thus the "mutation of Waagen" arises continuously through the inner working or tendency, the "*Mutationsrichtung*" of Neumayr.

It was not until 1894 that William B. Scott brought Waagen's term "Mutation" to the notice of vertebrate palæontologists in this country, in antithesis to Darwin's term Variation. Waagen's "Mutation" means one thing, Darwin's "Variation" means quite another, as pointed out by Scott above. The term Mutation in Waagen's sense is now widely but not universally used by palæontologists to designate intermediate gradations of minor taxonomic rank which are observed in ascending or descending series of animals to connect the larger stages of evolution which we call Species. As an ele-

mentary species a "Mutation" of Waagen is comparable to a "Mutant" of De Vries in external appearance, but not in mode of origin, because one arises through a continuous "*Mutationsrichtung*," while the other arises through accidental germinal saltation. To my mind the continuous or discontinuous mode of origin either of a "mutation" or of a "mutant" is of small account as compared with the fortuitous or orthogenetic nature of the impulse in the germplasm which gives rise to it.²

So far as I know all observers of the hard parts of extinct animals, whether vertebrate or invertebrate, confirm this classic observation of Waagen, and many in this special field of observation also confirm the "*Mutationsrichtung*" of Neumayr. So far as I personally have observed, this principle of "*Mutationsrichtung*" is especially dominant in the origins of characters; here at least other interpretations are not applicable; there is no question of Selection between two alternatives, adaptive and inadaptive, because the inadaptive does not occur, the whole process is adaptive and the difference between two organisms is the rapidity and direction with which the "*Mutationsrichtung*" is acting. This is the same in the hard parts of the molluscs *Ammonites*, *Paludina*, and *Planorbis*, as it is in the mammals *Equus*, *Rhinoceros*, and *Elephas*.

3. THE ORIGIN OF NEW PROPORTIONS

In the evolution of proportions, that is, proportions in the different parts of skeleton and skull as in *Sphenodon*, *Deinodon*, *Struthiomimus*, *Diatryma*, it appears probable that Selection may be constantly working on all adaptive fluctuations of proportion in connection with ontogenetic modifications in proportion which are also adaptive, as in the classic case cited by both Darwin and Lamarck of the length of the neck of the giraffe.

² F. A. Bather in 1905 (*Proc. Geol. Soc.*, Vol. 61, pp. lxxii-lxxiii) most clearly elucidated Waagen's conception of the Formenreihe and of the Mutation in *Ammonites*.

It has been demonstrated experimentally that the limb proportions in the brief life of a dog may be modified from the cursorial to the saltatorial type by amputating the fore limb. This is a process of reciprocal Modification and Selection which Osborn, Baldwin, and Morgan term Organic or Coincident Selection. I have devoted an immense amount of study to the causes of the evolution of proportion and have come to the conclusion that orthogenesis in the evolution of proportion may be apparent rather than real. In other words, whenever a character assumes a survival or elimination value, it may develop very rapidly through the selection of fluctuations in the right direction and may result in apparent but not real orthogenesis.

4. SUMMARY AS TO ORTHOGENESIS

The visible "mutation of Waagen," or "definite variation" or "rectigradation" of Osborn appears to depend on the "Mutationsrichtung" in the germ-plasm. The final question in my mind, as in yours, must be, if such a "*Mutationsrichtung*" exists, is it the "internal perfecting tendency," is it the "vitalism," is it the "creative evolution" which the majority of biologists are so skeptical about?

I observe that it is not. I observe that while the "*Mutationsrichtung*" is a real process, it differs from any kind of internal perfecting tendency in the fact that it consists in an adaptive reaction to the particular environment in which a series of organisms is placed, or to which it migrates. For example, the internal perfecting tendency to arboreal life does not manifest itself when the animal seeks an aquatic life. Conversely, aquatic adaptations are not constantly springing up among arboreal mammals. Observations on fossil forms have led to Dollo's remarkable generalization regarding "alternate adaptation," which renders any form of internal perfecting tendency in any predetermined direction inadmissible.

Summary of Observations.—In the hard parts of animals orthogenesis is observed both in the origin of new adaptive characters and in the evolution of proportions. (1) The induction as to cause may be different in the two cases. (2) In the origin of new adaptive characters orthogenesis is attributable to definite germinal tendencies. (3) The origin of changes of proportion which are subject to *modification* may be partly attributable to Organic Selection. (4) There is positive disproof of an internal perfecting tendency (Vitalism) in either the origin of new characters or the origin of proportions. (5) There are certain changes of length and breadth proportion both in the shells of invertebrates and the skulls of vertebrates which can not be explained by Organic Selection. (6) There is very strong support in fossil series for Selection incessantly acting on all characters of survival or elimination value.

The above six principles are those which I have derived from forty years of continuous observation; they are actual modes of the mechanical evolution of new species for which we have no theoretic explanation, unless it be that of Organic Selection in the single case above noted.

Summary of Opinions.—I may add as a matter of personal opinion and hypothesis three points: *first*, that we are as remote from adequate explanation of the nature and *causes of mechanical evolution* of the hard parts of animals as we were when Aristotle first speculated on this subject three hundred years B.C.; *second*, that the chief outlook for experiment is in the domain of physics; *third*, that the explanation, if ever it is to be found, is to be along the lines of four systems of energy (=Tetraplasy, Tetrakinesis, Osborn) which surround the origin and development of every character in every organism; *fourth*, I think it is possible that we may never fathom all the causes of mechanical evolution or of the origin of new mechanical characters, but shall have to remain content with observing the modes of mechanical evolution,

just as embryologists and geneticists are observing the modes of development, from the fertilized ovum to the mature individual, without in the least understanding either the cause or the nature of the process of development which goes on under their eyes every day.

In conclusion, it is the great biological achievement of the last half century that palæontologists have discovered *how* new characters and new species originate. It may be the achievement of the experimental biologists during the next half century to explain *why* new characters and new species originate.

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THE EFFECTS OF ENVIRONMENT ON ANIMALS¹

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As Henderson² has pointed out, the environment on the surface of the earth is suited to, and largely responsible for, the existence of living organisms. After an organism comes into existence, it strives to live in harmony with its immediate environment. An organism is a "system of activities"³ which devotes its energies primarily to three functions: (1) capturing energy for and releasing energy from its own system, (2) protecting its system from injury, and (3) producing other systems of activities similar to itself. If possible an organism reacts with its environment in such a way that its system continues to exist and carry on its three primary functions. It is limited in its responses to a particular behavior pattern, inherited from the system from which it came, but in general it reacts in such a way toward its environment that it selects by trial the optimum conditions for its own existence. In other words, an organism generally responds in an adaptive way and selects the best environment that it can. If the behavior patterns of certain systems, similar or dissimilar, are well suited to a particular environment, such systems often are "successful." They may take possession of the environment, perhaps exterminating other systems, and, thus demonstrating their "fitness," constitute what ecologists call a climax formation. Every organism in such a group must remain a system of activities and must make continual physiological adjustments to keep in harmony with the environment, or it can not continue to exist. Each organism assumes a

¹ An address before the Geographical Society, University of Wisconsin, January 11, 1922.

² "The Order of Nature," Cambridge, 1917.

³ This definition is not intended to exclude the possibility that an organism may be more than matter and energy. It may contain an entelechy or something similar, but as yet there is no scientific proof that it does. The limitation, and value, of science is that it must always deal with facts.

particular internal pattern that consists of a graded series of metabolic activities which (*de Child*) is a direct response to stimuli received from the environment.

In responding to environment plants and animals show fundamental similarity. Many plants adjust themselves to their surroundings by assuming the form that best suits them to the particular space in which they happen to take up a sessile life, and many animals secure a place which is suited to their system of activities by moving about until they find it. This difference between plants and animals is largely due to the fact that the former usually are able to subsist on inorganic foods, while the latter require organic substances as a basis for their metabolic activities. However, animals often respond to the environment by assuming a particular growth form, and plants have many motile systems of activities that find favorable environments through active or passive migrations. Being trained as a zoologist and knowing little of the activities of plants, I gladly take the task assigned to me—"to discuss the effects of environment on animals"—but I can not refrain from expressing my opinion, that there is no essential distinction in this connection between the two great kingdoms of life.

Animals are continually active and must continually react with the environment. Alcock⁴ said, "the three great exigencies: to find something to eat, to avoid being one's self eaten, and to disseminate one's species, give rise to a perpetual struggle in which the fittest are successful." The environment furnishes matter and energy to maintain the activities of each system and a considerable quantity of both is necessary. A silkworm during its short life eats food amounting to 86,000 times its own weight at the time of hatching. Animals take the most diverse materials from the environment and use them to build substance or furnish energy. The clothes moth flourishes on a diet of wool, which consists entirely of keratin. From this almost pure, and to most animals wholly indigestible, pro-

⁴ "A Naturalist in Indian Seas." London, 1902.

tein substance the moth makes carbohydrate, fat, and water to supply the needs of its system. The bee moth subsists on bee comb, which contains less than one per cent. of protein and a large amount of rather insoluble wax. Ants not only acquire food from the environment, but give up what they have already swallowed to their fellows, even when they are hungry themselves. In this case the "system" of the colony is more important than that of the individual.

In order to keep their systems of activities intact, animals have adopted many means to escape dangers. There are lurking enemies, physical changes, accidents, insidious parasites to be met or avoided continually. A walking-stick spends nine-tenths of its life in a "perfectly quiescent" state, depending on being overlooked by hungry enemies. A house fly escapes through endless agility. A rotifer avoids drying up by secreting a cyst about itself, and may remain dormant for years. Many animals are able to change the usual rate of their metabolic activities in response to changes in temperature and pass cold periods in a hibernating state.

Animals, before all things, use the means they possess in order to perpetuate their particular systems. New individuals must continually be started on new life cycles and such recreations involve reorganizations of systems, changes in metabolism, and various responses by organisms to the environment. Such qualities as odors, colors, and songs may be very important for the survival of a race. A male moth will migrate a mile or more to find a mate—attracted by her odor. The daily routine of seeking and escaping dangers is often neglected by animals when the survival of their race is concerned. Greedy penguins allow any youngster that comes to feed from their crops. An adult bull seal takes no food from May to August, but devotes all his energies to the defense of his rookery. The male gaff-tops'l catfish takes the eggs from his mate and carries them in his mouth for ninety days—denying himself food in order that his offspring

may survive. The little spider that spins a cocoon under stones guards her treasure with watchful care and, if she is compelled to leave her cocoon, spins a ground line as she runs in order that she may return without delay. A male spider dances, postures, and uses all his arts to secure a mate. As soon as he has mated, Nature usually sacrifices his life to his offspring—for his hard-earned mate devours him if she can.

Thus it is wherever one considers animals. There is adjustment, frequently of a very specialized type, to environment. The wonder of it all is the degree of adaptation that animals show. In speaking of food relations Semper⁵ said, "there is scarcely a constituent of the earth's crust, whether on land or in water—not an animal nor a plant, whether living, dead, or even in decomposition—which does not afford nourishment to some living animal." The first more or less self-evident generalization justified by this discussion may be stated as follows: *Animals are adapted to the environment.*

That animals are adapted, probably no one disputes, but there has been much controversy as to the means by which they have become adapted. There appear to be three effects that it is possible for the environment to produce in animals: (1) a direct transformation or modification of the living system of activities, (2) the destruction of systems unsuited to the environment and the "survival of the fittest," and (3) the migration of systems from unfavorable to favorable environments.

Animals are modified by external changes and may even take on different forms to suit different environments. Sponges and corals growing in deep water usually have a branching form; the same species in shallow water form flat, encrusting growths. The brine-shrimp, *Artemia salina*, is a classical instance of an animal that has many forms, and these are rather closely correlated with the salinity of the water in which it lives. Sumner⁶ and Shel-

⁵ "Animal Life as Affected by the Natural Conditions of Existence," N. Y., 1881.

⁶ Bull. U. S. Bureau of Fisheries, 1910.

ford,⁷ working independently, have shown that very slight structural differences that distinguish closely related species of amphipods and tiger-beetles are correlated with distinct habitat preferences. The structure and physiology of animals are modified by environment—the structures and activities of the systems are changed. Different species may possess almost identical structures, but show specificities of behavior in relation to environment.

Darwin made much of the struggle for existence among animals, pointing out that many species hold their places on the earth through wide dissemination and selective survival. One who has seen the strangler trees gaining a foothold in the tropical forest, the fiddler crabs fighting to hold a favorable place on an ocean beach, or the oysters in an overplanted area striving to survive, can not doubt that there is such a struggle. More animals are produced than can find a place to exist, and in general those survive that are best suited to the environment that is available.

Animals are not always obliged to adjust themselves to the environment or struggle for a favorable place to live in it. They migrate from situations where their systems can not well carry on activities to some spot where conditions are more propitious. In such migrations animals have very definite relations to the environment. They are limited by their reaction pattern to certain habitats; they must disperse from their "centers of origin" through "highways," and are prohibited from migration into certain regions called "barriers." Barriers are areas where certain environmental factors vary beyond the limit of toleration for a species. A "center of origin" as usually understood by geographers, may be the real place of origin of a species or it may merely represent the locality where the most environmental factors are favorable. In general a uniform environment covering a wide range of territory permits the species suited to such an environment to have a wide geographic range.

⁷ *Biol. Bull.*, 1911.

Variable species usually have wider ranges than unvarying, because they can adapt themselves to more environmental variations.

A second generalization is appropriate here: *Animals become adapted to environment by (1) transformation, (2) selective survival from an overpopulated condition, (3) migration from unfavorable to favorable situations.*

It will be profitable now to examine two or three typical associations in order to study animals in action with the environment. If, in this connection, one thinks over the great responses that animals have made to environment in the past, he will probably conclude that the greatest habitat change has been that from water to land. It is generally supposed that life first appeared in water. As a habitat, water has certain inherent advantages—the chief of which is perhaps the slowness with which temperatures change. It also has certain disadvantages, the most important of which are probably the variability of its dissolved gases (the higher the temperature, the less gas can be held in solution) and its general solving power, which makes it a transporting medium for all sorts of substances, some of which are poisonous. All animals require a more or less constant supply of water and of oxygen for metabolic processes. When animals forsook the water for land habitats, they gave up surety of water supply and conditions of reasonable thermal stability. What did they get in return? Apparently nothing but a stable gaseous condition for respiratory needs. The danger of desiccation and the wide variations of temperatures incident to land life were apparently compensated for by this gaseous stability. Yet the attractions of the water have at times led many animals, like the aquatic insects, that had become adjusted to life on land to revert to aquatic habitats. In the past races have doubtless many times become adapted by transformation, selection or migration on account of the advantages or disadvantages of one of two habits.

If one walks along a rocky shore, where the ocean

waves and tides sweep, he may be surprised to find an abundant fauna in the " 'tween-tide " zone. The moving water, teeming with microscopic organisms, brings an abundance of food to those animals that are able to stand the beating of the waves and the alternate submergence and exposure due to the ebb and flow of the tides. A rocky wall along the sea shore is no place for weaklings. One minute the blistering sun bakes the exposed animals; the next, the rising tide has covered them with cold water. The waves beat ceaselessly. The changing seasons bring ice and torrid heat. How are the animals on these rocky shores responding to the environment? Here one finds a variety of hardy species which, though not closely related genetically, have many characteristics in common. There are sponges, anemones, hydroid colonies, barnacles, mussels, snails, small crustaceans, and a few scavenger crabs. These animals for the most part obtain their food by net fishing or by straining water through their bodies. They are mostly attached firmly to the rocks, and thus withstand the violent movements of the food-laden water. The barnacles, sponges, and hydroids are grown fast; the anemones and snails have sucking discs that enable them to adhere firmly; the crustaceans have claws for attachment and hard armor covering their bodies. Some of these animals are small and can easily hide in crevices; some of those of larger size, like crabs, are able to migrate to other habitats during violent storms. If an animal is attacked, it is advantageous for it to be able to receive stimuli with facility from all directions of the compass, and, as would be expected, many of the animals on rock beaches are radially symmetrical. Radial symmetry has marked advantages for sessile animals, but puts a weighty limitation on psychic development. An animal that is able to perceive stimuli equally well, through equally efficient sets of sense organs that are symmetrically disposed about a central axis, is never able to develop its power of paying attention to any considerable degree. Its simple mind, if such an animal may be said to have

a mind, must attend now to a stimulus received from one side, now to that on another. Such vacillation is not conducive to the development of higher types of mental life through the delegation of psychic authority to one nervous center. The rocky ocean shores, then, put a premium on radial symmetry and thus as an environment tend to foster psychically unprogressive animals. The barnacles, that appear to have come from progressive, bilaterally symmetrical ancestors, have become degraded with the taking on of the sessile life and radial symmetry that suits them so well to wave-beaten shores.

The ebb and flow of ocean tides have a pronounced effect on shore animals. Those species that are not able to survive alternating exposure to the desiccating effects of air of varying temperatures and the activity of violently moving water of rather constant temperature can not exist on rocky shores. This fauna must be resistant, and is so. An anemone can be kept out of water for a week—until it looks like a dried raisin; or kept in a tightly corked bottle for ten days, and when replaced in the ocean appear to be perfectly normal in an hour or two. Such an animal will not readily succumb to the exposure between tides or even to the stagnation likely to occur in a beach pool that is cut off from the ocean during a prolonged period of low water. The barnacles and molluscs on rocky shores are protected by heavy calcareous shells. Flattely^s has suggested that land animals perhaps arose in the past on ocean beaches as a result of the resistance developed during exposure between tides.

As a whole the environment occurring on rock beaches offers abundant food, but hard conditions for life. The fauna is highly adapted to resist the two important environmental factors—moving water and exposure to variable conditions—and in this adaptation the fauna has incidentally but of necessity become unprogressive and devotes most of its activities (1) to feeding rapidly when the opportunity comes, (2) to resisting, (3) to resting.

^s *Science Progress*, 1921.

One does not imagine such a fauna as developing, even through countless ages, great appreciation of beauty, or of any of the æsthetic qualities of "higher" animals. The adaptations here are to resist the unfavorable in the environment, and still live.

If a man walks in a tropical forest, he is amazed at the abundance and variety of the life about him. He may see a certain species of tree in one spot and not encounter another like it for a mile. Meanwhile he has seen a hundred other species of trees. What is the striking environmental factor in this forest? It is life itself! The environment is favorable for so many systems of metabolic activity that hundreds of kinds of animals are ready to live in it—if they can find a place. Is there a struggle; is there adaptation? Nowhere on the earth are these responses to environment more striking. Most of the struggles to live in the forest are competitions with other living systems that are trying to continue to exist. And the adaptations are not often for resisting, for eating, for resting. Think of all the animals in the tropical forest—is there one that is radially symmetrical? Here keen senses are at a premium. Life has always depended upon seeing, hearing, feeling better than something else. Lately it has come to depend upon thinking better than something else. And the climax of adaptation in this tropical forest has been the greatest thinker of the ages.

A third generalization appears to be justified: *Each habitat, representing environment, limits the patterns of the systems of activities that may persist from reactions within it. The type of adaptation is set by the environment.*

Environment has a quality that any system of activities that attempts^o to live in it must respond to. This is its changefulness. The paleontologists say that environment punishes too much adaptation by changing. I think it is proper to say that the chief cause assigned for the

^o The writer realizes that "attempts" may be interpreted as teleological—and rejoices in the sinfulness of it. If an organism does anything, it strives to keep on existing. As far as it possesses means, it responds to whatever interferes with living.

dying out of extinct types of animals is "over-adaptation," or better "too much specialization." A system of activities, as represented by an organism, can not depend absolutely on another system of activities, as represented by environment. The organism changes and the environment changes too. If the environment continues for a time in a fairly stable condition, an animal may become adapted to it to such a degree that, if the environment then does change, the animal can not respond enough to continue to live. The wood frogs in the United States breed when the water is at freezing temperatures; frogs, belonging to the same genus as the wood frog, that live in Cuba die when the temperature falls below seven degrees. These frogs are adapted to different environments and those in Cuba will be in greater danger of extinction if there is a prolonged cold period.

There is a general tendency among animals to find success during conditions of stability. Certain arthropods left the water and attained stable respiratory conditions and freedom from water-soluble poisons by going on land. Later, certain of these arthropods again gained a thermally stable environment in the water and continued to enjoy a stable gaseous environment by carrying air into the water with them. When any race of animals attains a stable environment, it may become specialized to it. We see a manifestation of the same type in the psychology of man. It is "human nature" to desire stability—to be free from care and worry; to know where one stands.

On the other hand, continual change is a stimulus to progressive response—in fact, one is tempted to say that lack of change is injurious to living organisms and that changes often stimulate living systems to renewed activity. Payne kept fruit flies continuously in the dark; Calkins and Woodruff maintained protozoans on unvarying culture media. All these investigators agreed that lack of variation in the environment was injurious. This raises a dilemma—on one hand animals tend to become highly adapted (or specialized) when the environment is

stable, and on the other hand a changing environment is a stimulus to progressive changes in organisms. A few animals have lived for ages in a stable environment. Thompson cites the brachiopod, *Ligula*, as a "supreme instance of static racial inertia." However, most animals must live in environments that change. How do these respond?

It is a matter of common knowledge that animal systems of activities can become adapted to changes in the environment, even when such changes constitute new racial experiences. By taking increasing doses of certain poisons at regular intervals animals develop enough immunity to be able to take daily a dose which in the beginning would have been fatal. If a pigeon is fed nothing but meat the lining of its stomach changes its character and the bird's metabolic activities become adapted to an unusual diet. Many other instances of acclimatization to new conditions might be cited.

Every physiographer knows that earth environments change by succession. Land forms erode and water forms fill up with sediment. Physiographic succession brings about a succession of environments, or habitats. These are successively occupied by different groups of plants and animals and there is thus an ecological succession, which is a succession of species or groups of species. Shelford has worked out excellent examples of ecological succession in the streams and ponds along the shore of Lake Michigan. Pioneer species of animals invade habitats soon after they are formed, and as the habitats change the pioneer species are succeeded by others that are adapted to later stages in physiographic succession. Ecologic succession is a succession of species; animals do not change as the environment changes, but die or migrate to more favorable localities. Animals do not appear to have special means for adapting themselves to such changes.

There are other types of succession, however, to which animals show striking adaptation. The types are all rhythmic (seasonal, monthly and daily) and depend pri-

marily upon the motion of the earth and moon. As the earth makes its annual journey around the sun, the animals of temperate and polar regions, and to a less extent those in the tropics, are subjected to seasonal changes in environment. These changes are related chiefly to temperature, available moisture, and food. Animals generally respond to such environmental variations by adjusting appropriate activities to favorable times. In general winter is a season for resting; spring, for mating and propagation; summer, for feeding and growth; and autumn for fructification. Seasonal succession is a succession of stages in life cycles. The seasonal rhythm has a short enough period to permit animals to become adapted to it. Their systems of activities vary to fit the seasons. Every one is familiar with the seasonal migrations of animals. The arctic tern travels from pole to pole, and thus always lives in sunshine. Many animals do not migrate, but pass the winter in a dormant condition. In the tropics animals frequently aestivate during the annual dry season. Now many of these seasonal responses are certainly due to stimuli received from the environment. The little *Daphnias*, that live in fresh-water habitats the world over, usually have long helmets in summer and short helmets in winter, but long-helmeted forms can be made to produce short-helmeted offspring in summer by keeping them at low temperatures. In this instance the effective stimulus appears to be thermal in nature. But animals are adapted to seasonal succession beyond merely responding as far as they are able to stimuli that come with rhythmic changes without their bodies. The living system apparently has a rhythm of its own that is adapted to the seasons. Smallwood¹⁰ kept a female dogfish (*Amia calva* Linnæus) in an aquarium, practically without food, for twenty months at rather constant temperature. During this time the fish twice took on its bright nuptial coloration. Another instance of similar nature has come to the notice of the writer. A tame spermophile, *Citellus tridecimlineatus* (Mitchill), was kept in a steam-heated

¹⁰ Biol. Bull., 1916.

house for four years. In the autumn of the first year it became very fat and stored a large quantity of food in its burrow. About December 1, it went into its burrow, closed the opening, and remained underground for 119 days. The following autumn the spermophile behaved in a similar way but remained underground for only 28 days. It did not hibernate during the two years following. This animal had an established seasonal metabolic rhythm that was correlated with seasonal environmental changes, but the rhythm had a physiological basis for it persisted when appropriate environmental stimuli were not present.

The rotation of the moon about the earth introduces certain rhythmic variations into the earth environment to which animals respond in adaptive ways. Such responses are of course not due directly to the moon as such, but to effects of the moon's motion on matter belonging to the earth. The famous Palolo worm and various other marine annelids come from their hiding places to spawn only during certain phases of the moon. In these worms the eggs do not ripen except when the moon is new or full; the internal activities respond to outside changes, chiefly referable to tidal variations, and a physiological rhythm is established.

The earth rotates on its axis and thus the animals on its surface are subjected to alternating light and dark. Animals readily respond to this short-period rhythmical change. Every one is familiar with nocturnal and diurnal animals. They are adapted to rhythmical environmental changes to such a degree that they may keep on responding periodically when the environment does not change. Keeble and Gamble¹¹ have described an interesting shrimp (*Hippolyte varians*) that has day and night color phases. During the day this shrimp matches the background on which it rests with a high degree of accuracy, assuming quite a variety of colors and patterns. At night it turns green, regardless of its background. When kept continuously in light it undergoes rhythmic color changes at about the time periods that correspond to day and night

¹¹ *Phil. Trans.*, London, 1904.

for two days; and makes similar changes in the absence of light for about a week. There is a physiological rhythm that corresponds to periodic environmental changes.

A fourth generalization must again relate chiefly to adaptation—*Though animals possess considerable power of adjustment to new or changed factors in their environment, they apparently do not usually become adapted as species to physiographic changes, but are eliminated by the variation of factors beyond their limit of toleration. One species or group of species succeeds another during physiographic succession. However, animals do respond in an adaptive way to rhythmical daily, monthly and seasonal successions.* Some animals show adaptive responses to rhythmical environmental changes only once during their life cycle. Salmon, for example, do not migrate up rivers to spawn until they have reached a certain age. *Animals apparently become most specialized, or adapted to particular environments, when conditions are most stable. Even the striking instances of adaptations to rhythms show this tendency of adaptation to attain stability—in this case a regularly changing stability.*

Environmental changes have been important in their effects on the evolution of animals. In this paper it has been shown that living systems of activities are adapted to the environment; that they respond to the environment by transformation, selective survival, or migration; that each habitat limits the patterns of the systems that exist within it; and, that, though adaptation to environment may permit precise adjustment to rhythmical changes extending over considerable periods, and though animals generally become most specialized when conditions are most stable, there is no evidence that living systems are caused to change from one species to another by the transformations of habitats due to physiographic succession. The pattern of evolution is set by environment, but there is little or no evidence that changing environment causes adaptive variations of such a degree that new species are produced. Animals adapt them-

selves to environment by changing their systems of activities, but such responses are apparently limited in extent to the inherent possibilities of variation already within the system. Animals have great powers of adaptation to environment, but are not fundamentally changed by it. Environment permits evolution and controls its course, but does not appear to cause it. If variations fit environment, they are adaptive; if they do not, systems cease to exist. Environment does not appear to cause variation. The living mechanism still holds the mystery of variation within itself. Until there is conclusive evidence, this one great remaining problem of evolution can not be solved. Yet, notwithstanding this lack of evidence, there are still those who believe the environment does cause evolution—though their only foundation for such belief is what Bergson calls “intuition.” Until there is proof, science, if it would be scientific, must keep in mind that these “faithful” believers may be right, and be content to wait, perhaps a hundred thousand years—for evidence.

SUMMARY

1. Animals are systems of activities that are adapted to environment.
2. Animals become adapted to the environment by transformation, selective survival, migration.
3. Each habitat limits the patterns of systems of activities that may result from reactions within it. The type of adaptation is set by the environment.
4. Though animals possess considerable power of adjustment to changes in environment, there is no evidence that they became adapted as species to slow changes due to physiographic succession. They do respond to rhythmical daily, monthly, and seasonal changes in an adaptive way. Animals appear to become most specialized, or adapted to particular environments, when conditions are most stable.
5. Environment permits and directs evolution, but does not appear to cause it by forcing the acquirement of new characters.

A SUMMARY OF THE FOOD HABITS OF NORTH AMERICAN COLEOPTERA

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THE Coleoptera or beetles contain a very large number of species and show a great diversity of habits. Most of them are terrestrial and they live under almost all conditions where insect life is possible. The economic status of this group of insects is important. To the Coleoptera belong some of our most pernicious agricultural pests as, for example, the cotton boll weevil, which has caused such ruin in the cotton belt, the Colorado potato beetle with its familiar destructive activities and various other species which attack forests and field crops with varying degrees of intensity. However, many species of Coleoptera are engaged in useful activities and it is the purpose of this paper to summarize briefly, and in a very general way, the food habits of the families in this order.

For the purpose of convenience in handling and for the sake of simplicity, the families have been grouped into a few important classes and the placing of each family was based mainly on the predominating larval activities of its members. In some families considerable variation occurs in the food habits of the different species. For instance, in the *Scarabæidæ*, some are destructive to green vegetation and others thrive on vegetable decay. On the whole, however, their activities are saprophytic and for this reason the entire family was placed in the group Saprophaga. The *Staphylinidæ* were placed in this group also, although this family contains members which live in fungi, in animal and vegetable decay, in the nests of ants and some which are predatory. In quite a few of the families, the activities of the species are practically identical.

The classes into which the families are grouped are as follows: Phytophaga, Saprophaga and Harpactophaga. In addition to these three important ones, the species attacking mammals and those whose family habits are

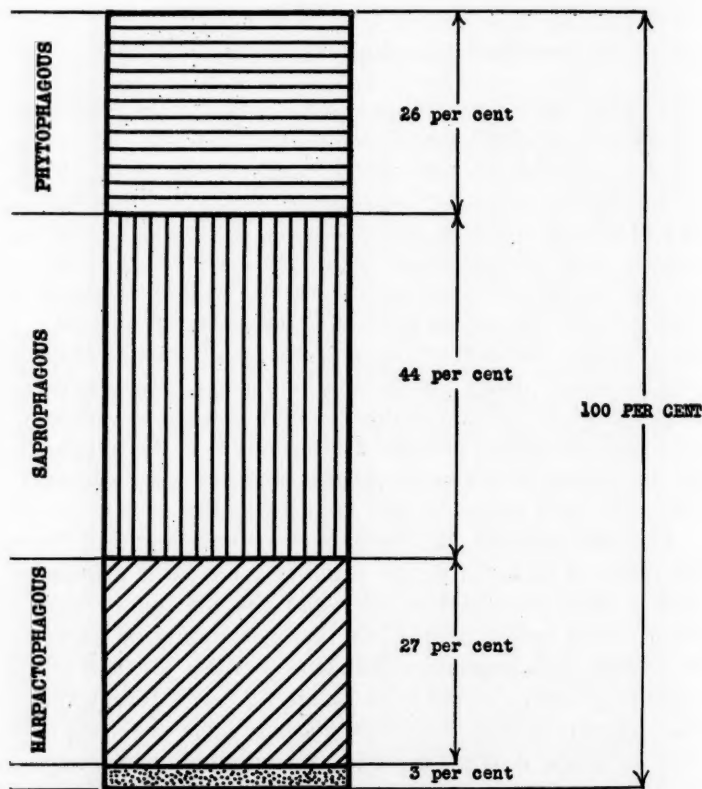


Diagram illustrating the comparative abundance of the various types of food-habits in the Coleoptera.

obscure have been grouped separately. In the Phytophaga have been placed those species which feed upon the higher plants. In the Saprophaga will be found those forms which feed for the most part upon disorganized tissue, vegetable and animal decay and such

species which remove or change the form of animal and vegetable remains and aid in reducing such substances into shape for assimilation by plants. While not strictly belonging to this group, species feeding on low forms of plants such as fungi and those living on dry vegetable and animal matter have been included for the sake of convenience and in order to avoid numerous subdivisions. In other words, the term Saprophaga is used in a very broad sense.

The Harpactophaga contains the predacious and carnivorous species, of which there are a great number, and whose activities help to preserve a natural balance between certain groups. Many of them are general feeders, appearing to be not particular whether their prey is a plant feeder or another predatory form. However, in some families, such as the *Coccinellidae*, there is a decided specialization as to the prey, and such a group is very often an important specific check to unusual increases in the numbers of plant lice. The Coleoptera attacking living mammals are few in number. The species in the family *Platypsyllidae* consists of a wingless beetle found on beavers. In the *Leptinidae*, the species have been found in the nests of field mice and bumble-bees, but their exact habits are somewhat obscure. It has been suggested that the bumble-bee nest is the natural home and that the field mice afford transportation from one nest to another.

The last group is made up of those families of which little or nothing appears to be known concerning their food habits. While this same lack of information is true for a large number of individual species placed in the other groups, yet enough is known of their general family habits so that little risk is run in placing them as family units. This, however, could not be done with any certainty in the case of the last class and they are presented simply as a group difficult to classify from a food standpoint.

The following tables show the name of each family, the number of species in that family described up to and in-

cluding 1918 and a brief statement indicating the more important food habits. The information in the first two columns was compiled from the recently issued "Catalogue of the Coleoptera of America North of Mexico" by C. W. Leng.

PHYTOPHAGA

Family	No. Species	Habits
Lymexylidæ	2	Bore in hard wood.
Buprestidæ	379	Wood borers in healthy and unhealthy trees.
Cerambycidæ	1,123	Borers in dead, dying and healthy trees and plants.
Chrysomelidæ	974	Feeders on vegetable tissue.
Mylabridæ	93	In seeds.
Brentidæ	6	In wood.
Belidæ	1	Like <i>Curculionidæ</i> .
Curculionidæ	1,839	Feeders upon vegetable tissue.
Platypodidæ	5	Boring in trees.
Scolytidæ	379	Borers in wood, healthy and sick trees.

SAPROPHAGA

Family	No. Species	Habits
Silphidæ	137	Scavengers in dead animal and vegetable matter, in fungi.
Clambidæ	6	Same as above.
Orthoperidæ	57	In decaying vegetation, under bark, etc.
Staphylinidæ	2,748	Varied, in ants' nests, in fungi, in decaying animal and vegetable matter, etc., predatory.
Pselaphidæ	355	Varied, in ants' nests, under vegetable decay, in wet moss, in rotten stumps, etc.
Clavigeridæ	7	Same as above.
Ptiliidæ	83	In decaying vegetable matter, excrement, fungi.
Sphæriidæ	3	In vegetable decay.
Scaphidiidæ	50	In rotten wood, fungi.
Sphæritidæ	1	Same as <i>Silphidæ</i> .
Cupesidæ	4	Under bark, in dry wood, may be predaceous.
Ædemeridæ	49	In timber cast up by sea.
Mordellidæ	142	Varied, adults on flowers, larvæ in dead wood, fungi, stems of live plants.
Pythidæ	17	In timber.
Pyrochroidæ	11	Under bark of tree stumps.
Euglenidæ	39	In dead wood.
Cerophytidæ	2	Probably like those of <i>Elateridæ</i> .
Cebrionidæ	9	Probably like those of <i>Elateridæ</i> .
Elateridæ	576	In decaying wood, in soil on roots of grasses, etc.

Melasiidæ	57	In dead trees.
Throscidæ	25	Like those of <i>Elatridæ</i> .
Dascillidæ	29	On roots of aquatics, in fungi.
Dermestidæ	129	In dried animal matter.
Ostomidæ	64	Varied, under bark, in granaries, in fungi, predaceous.
Nitidulidæ	132	Sap beetles, on flowers, predaceous.
Rhizophagidæ	14	Probably like above.
Monotomidæ	36	In ants' nests, probably have no relations with ants.
Erotylidæ	71	Mainly in fungi.
Cryptophagidæ	135	In fungi and decomposing vegetable matter.
Mycetophagidæ	32	Under bark, in fungi.
Colydiidæ	84	In fungus covered wood.
Lathridiidæ	104	In fungi.
Mycetæidæ	4	In fungi.
Endomychidæ	34	In fungi.
Phalacridæ	117	Under bark, on flowers.
Alleculidæ	124	Larvæ in rotten wood, adults on leaves, flowers.
Tenebrionidæ	1,139	In dry vegetable matter, fungi.
Lagriidæ	17	Probably like above.
Melandryidæ	81	In dry wood, fungi.
Ptinidæ	37	In dry animal and vegetable matter, wood, drugs, etc.
Anobiidæ	233	In dry vegetable matter.
Bostrichidæ	61	In dry wood.
Lyetidæ	16	In dry wood.
Sphindidæ	6	In fungi.
Cisidæ	85	In fungi.
Scarabæidæ	996	Varied, in decaying vegetation, on roots of plants, on green vegetation.
Lucanidæ	30	In decaying wood.
Passalidæ	2	In decaying wood.
Platystomidæ	62	On dead wood, in fungi.

HARPACTOPHAGA

Family	No. Species	Habits
Cincindelidæ	114	Predaceous.
Carabidæ	2,165	Predaceous.
Omophronidæ	15	Predaceous.
Haliplidæ	41	Aquatic, predaceous.
Dytiscidæ	333	Aquatic, predaceous.
Gyrinidæ	41	Aquatic, predaceous.
Hydrophilidæ	190	Predaceous.
Seydmenidæ	174	Feeding on acari, in ants' nests.
Histeridæ	384	Found in same situations as scavengers but probably predaceous.

Lycidæ	50	Carnivorous as larvæ.
Lampyridæ	52	Larvæ carnivorous, adults on flowers.
Phengodidæ	23	Larvæ carnivorous, adults on flowers.
Cantharidæ	155	Larvæ carnivorous, adults on vegetation.
Melyridæ	321	Predaceous, adults on flowers.
Cleridæ	181	Predaceous, adults on flowers.
Corynetidæ	38	Predaceous.
Cephaloidæ	8	Probably similar to those of <i>Cantharidæ</i> .
Rhipiphoridæ	26	Larvæ parasitic in ants' nests, on cockroaches.
Meloidæ	227	Larvæ predacious, adults on green vegetation.
Cucujidæ	85	Varied, under bark, predacious, in stored products.
Coccinellidæ	362	Predaceous.

ANIMAL PARASITES

Family	No. Species	Habits
Platypsyllidæ	1	Animal parasite.
Leptinidæ	3	Probably parasitic on mammals.

FOOD HABITS OBSCURE

Family	No. Species	Habits
Amphizoidæ	2	Aquatic.
Brathinidæ	3	
Telegeusidæ	1	
Micromalthidæ	1	
Eurystethidæ	3	
Pedilidæ	54	Probably like those of <i>Anthicidæ</i> .
Anthicidæ	191	On surface of earth like ground beetles.
Plastoceridæ	19	
Rhipiceridæ	6	In wood.
Psephenidæ	4	Semi-aquatic.
Dryopidæ	17	Aquatic.
Helmidæ	36	Aquatic.
Heteroceridæ	11	Semi-aquatic.
Georysidæ	2	In wet places.
Helodidæ	32	Probably aquatic.
Chelonariidæ	1	
Byrrhidæ	97	Habits obscure, on ground beneath cover, about grass roots.
Rhysodidæ	4	
Derodontidæ	5	
Murmidiidæ	5	
Monædidæ	1	
Monommidæ	6	

SUMMARY

	No. Species	Per Cent. of Total
Phytophaga	4,801	26
Saprophaga	8,252	44
Harpactophaga	4,985	27
Animal parasites	4	
Food habits obscure	501	3
	18,543	100

About 26 per cent. of the species of Coleoptera are phytophagous, most of this percentage being made up of the families *Curculionidae*, *Cerambycidae* and *Chrysomelidae*. Almost one half of the species of beetles, or 44 per cent., appears to be saprophagous for the most part and in this group the families *Staphylinidae*, *Tenebrionidae* and *Scarabaeidae* supply over half of the species. In the predaceous group, consisting of 27 per cent. of the total, the *Carabidae* with its 2,165 species is the largest single contributor. Thus almost three fourths of the species of beetles in North America are apparently engaged in what we call useful activities.

INDIRECT EVIDENCE FROM DUPLEX HYBRIDS
BEARING UPON THE NUMBER AND DIS-
TRIBUTION OF GROWTH FACTORS
IN THE CHROMOSOMES

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SUFFICIENT evidence has accumulated to indicate that the main features of the chromosome theory of hereditary transmission, as worked out for *Drosophila*, are applicable to plants. Peas, primula and maize have been the best materials so far to demonstrate linkage of factors in plants. Owing to the ease of culture, large number of seeds produced and the great genetic variability the maize plant is becoming very useful in this line of investigation. The agricultural importance of the plant and the large number of people working with it have already made the list of Mendelian factors definitely determined large and increasing rapidly. Due mainly to the industry of Professor Emerson and his co-workers at Cornell University, six linked groups are already visible in rough outline, some of which have a goodly number of factors fairly well located. It therefore seems pertinent to consider some indirect evidence furnished by this plant having a bearing upon the chromosome mechanism.

In working out the best means of utilizing inbred strains of corn for the purpose of increasing production it has been found to be advantageous to cross again two different first generation hybrids each of which were the result of combining two different self-fertilized families. Altogether four homozygous types, each differing from the other in many visible characters, are brought together in this way in a progeny which has an extremely complex composition. Assuming that the inbred strains have been reduced to complete homozygosity, the first generation hybrid is uniform. Statistical measurements show this

to be so. Theoretically, all the plants are hereditarily exactly alike. When such a hybrid with segregating gametes is again crossed with a similar first generation hybrid but having a different genetic construction, the result is a mixed lot of plants in which practically every individual differs in some degree germinally from every other.

This statement holds for any numbers that it would be possible to grow. Every inbred strain of maize, that has so far been obtained by continued self-fertilization with one progenitor in each generation, has differed in many ways from every other inbred line, whether they came originally from the same or different varieties. All the inbred strains coming from different individuals at the start show a noticeable increase in vigor when crossed and a rapid reduction of growth and great increase in variability in the immediately following generations when again self-fertilized. It is therefore not at all improbable that most of the self-fertilized strains differ from each other by a large number of genes in every chromosome.

If such is the case, then the duplex combination will have an extraordinary amount of genetic diversity. This may be made clearer in the following illustration. If, instead of being crossed, a hybrid was self-fertilized and there was only one factor difference in each pair of chromosomes, over one million plants would have to be grown in order to have an even chance of securing all the possible combinations (assuming maize to have 10 chromosomes). But with more than one factor in each chromosome the situation is far different. Two factors in each chromosome having a linkage ratio of 10 per cent. would necessitate 20^{20} individuals in the segregating generations to obtain the same result. This is calculated from the formula $[2(r+1)^{n-1}]^{2c}$ where $r+1$ is the linkage ratio, in this case 10 per cent., or $9+1$, n is the number of factors in each chromosome, and c is the number of chromosome pairs. This number of plants to be grown would require an area roughly 57,346 million times the total surface of the earth. But instead of being

self-fertilized, the hybrids with their segregating gametes are again crossed and certainly there are more than two factor differences in most of the chromosomes having varying degrees of linkage with each other. At present almost nothing is known about the heredity which the two first generation hybrids may have in common. But all the four homozygous types when crossed singly in the six possible combinations show about an equal amount of heterosis. The double-crossed combination shows no reduction in vigor of growth, but on the other hand this appreciably increased. This is due, however, in part to a better start as the plants come from large, well-nourished seeds grown on vigorous plants, whereas the first cross is handicapped in this respect.

The doubly hybrid plants are theoretically more diverse than self-fertilized second generation progenies coming from the same parents, but compared with the first and second generations the double cross has features of both. In respect to growth characters the plants are a group of many different first generation hybrids. Very little recombination can take place to allow recessive weaknesses to appear. In fact any recombination that does take place is probably out-balanced by an increase in heterozygosity in other factors. A critical comparison of such double hybrids with their parental first generation hybrids and with their second generation self-fertilized sibs in respect to variability of different characters ought to give some indication of the distribution in the chromosomes of the hereditary factors affecting growth.

In those factors which are independent of the growth of the plant the variability of the double cross should approach or exceed that of self-fertilized second generation. In those characters which are directly dependent upon the vigor of the plant the double cross should resemble more closely the first hybrid generation. Five characters have been taken and measured in three different but similar lots of plants. These are: number of rows of grain on the ear (pistillate inflorescence); nodes of plant, height of plant, length of ear; and pro-

duction of grain (weight of entire pistillate inflorescence with mature seeds). A previous study of a large number of first generation hybrids between inbred strains of maize has shown that the average number of rows of grain of the hybrids was increased 5.29 per cent. above the mean position of their parents; similarly nodes per plant 6.45 per cent.; height of plant 27.44 per cent.; length of ear 28.57; and total production of grain 180.00 per cent. The variability of these F_1 plants was slightly decreased below the parental average in nearly every case in respect to these characters.

Rows of grain and nodes are therefore much less influenced by the vigor of the plant than are the other characters, notably production of seeds, which is very largely determined by the amount and rapidity of growth. Assuming that the complementary action of dominant favorable growth factors is responsible for the vigorous growth of the hybrids, it would be expected that $F_1 \times F_1$ combination would not be as variable as the second generation resulting from self-fertilization in respect to production of grain per plant, provided a large number of essential growth factors were acting and that these were distributed rather uniformly throughout the chromosomes. On the other hand such characters as rows of grain on the ear and nodes per plant being largely independent of growth vigor, would not be expected to show a reduction in variability when compared with the second self-fertilized generation.

The distribution and statistical constants for the second generations grown from self-fertilized seed of the parental hybrids have been compared to the reciprocal crosses of the same parental hybrids in three different sets of plants. In each case the cross-fertilized seed, which produced the $F_1 \times F_1$ plants, and the self-fertilized seed, from which the F_2 plants were grown, came from the same ears. The two kinds of pollen were applied in a mixture at one time and the seeds separated by their color at maturity.

Without giving the extensive data upon which the

figures are based, the averages of the coefficients of variability of the $F_1 \times F_1$ and the F_2 families are brought together in table 1. With these are given some figures averaged from the F_1 parents. These are not from the exact first generation parents of the progenies used to

TABLE I

A COMPARISON IN VARIABILITY OF SINGLE FIRST GENERATION, DOUBLE FIRST GENERATION AND SECOND GENERATION HYBRIDS

Characters Measured	F_1		$F_1 \times F_1$		F_2	
	Ave. C.V.	Range P.E.	Ave. C.V.	Range P.E.	Ave. C.V.	Range P.E.
Rows of grain.....	8.90	.40-.98	12.76	.52-.65	12.31	.45-.82
Nodes of plant.....	5.54	.25-.73	5.88	.25-.27	6.20	.26-.33
Height of plant....	7.06	.25-1.04	6.20	.25-.33	6.92	.26-.40
Length of ear.....	13.83	.72-1.66	13.23	.41-.75	16.90	.69-1.03
Weight of grain....	24.13	1.15-1.42	26.99	1.19-1.44	32.68	1.11-2.31

give the other results in Table I. They are similar but were not grown in the same years. They can not be compared as closely to the $F_1 \times F_1$ and F_2 lots as these can be compared with each other. The coefficients for variability of the $F_1 \times F_1$ and the F_2 plants, averaged from three different combinations with a fairly large number of plants in each grown from seed of which the two contrasted kinds came from the same ears, are strictly comparable. The greater growth of the double hybrids as shown by the increase of the means makes comparison of the coefficients of variability somewhat unreliable. The appearance of the plants in the field supports the statistical data, as it is the uniform production which makes the hybrid plants so valuable for agricultural purposes. There is a noticeable difference between the double cross and the self-fertilized second generation in even size, similar appearance and general excellence as the plants are harvested in the field.

The figures show that the variability of the $F_1 \times F_1$ families is about the same as the F_2 families in rows of grain and nodes per plant. In height of plant, length of ear and weight of grain per plant, all characters which

are markedly influenced by the vigor of the plants, there is a reduction in variability. Particularly is this true of length of ear and weight of grain, which are fairly reliable measures of the plant's reproductive ability, which in annual plants sums up the organism's entire energy. In other words the plants are uniformly vigorous and are not dependent upon exceptional individuals for their high average position. This is indirect evidence that those hereditary factors which are concerned with the growth of the plants are numerous and widely distributed throughout all or many of the chromosomes.

As a means of corn improvement it would be highly desirable to bring together into a pure breeding homozygous condition all those factors which cause the hybrid plants to excel their parents. Such individuals should be even more efficient in their growth processes than the heterozygous combinations of the same factors because the determiners responsible for hybrid vigor seldom show complete dominance. The recombination of linked factors is a problem that demands the most careful attention of the plant and animal breeder. It is the closely linked factors which are the main concern. When the distance between any two loci is fifty units or more, then all the factors situated outside of these points are independent of each other in transmission and it makes no difference from the standpoint of recombination whether the factors are in the same or different chromosomes. Therefore the number and arrangement of the individual genes themselves seem to be more important than the number of chromosomes. Although as yet it is impossible to compare the numbers of factors in different species, it does not seem likely that the genus *Rosa* with 8 chromosome pairs is genetically less complex than *Nicotiana* species with 24 pairs. Some crustacean species with 84 pairs of chromosomes are contrasted with various mammals with 8 to 12. Even in the Arthropods alone the haploid number ranges from 2 to 100. It seems profitless to look for any significance in chromosome numbers. Leaving aside the matter of doubling of chromosomes any

differences that there may be are probably qualitative rather than quantitative. It is possible that there may be very little difference in the amount of essential hereditary material. But the word "amount" must be considered as equivalent portions. The visible size of the chromatin mass fluctuates greatly even at different stages of growth in the same individual.

Although the cytological proof of the chromosome theory is still so meager as to make speculation somewhat useless, nevertheless, looking at the matter from the standpoint of difficulty of recombination the important consideration is the number of fifty-unit lengths of chromosomes. However, the Morgan school unit of measurement, the one per cent. of crossing over, is not a stable unit, as they have shown that crossing over fluctuates rather disconcertingly, due both to environmental and germinal modifying factors. Detlefsen¹ finds the rate of crossing over between certain loci to be very profoundly altered by continued selection for high and low cross over stock. So that for the present the terms proposed by Haldane² of *morgan* and *centimorgan* as measures of chromosome length do not have any precise application. At the same time the rate of crossing over is the only measure available and can not be given up until a better one is found. The term *morgan*, referring to a one-hundred-unit length of chromosome is convenient but does not have the biological significance that a fifty-unit length of chromosome would have. Since every gene is independent in transmission from all other loci in the same chromosome more than fifty units distance from it, and has the usual Mendelian relation with them as well as with all the factors in the other chromosomes, the term *mendel* would perhaps be useful, if the employment of such terms can be justified at all. Applied in this way a *mendel* is a measure of chromosome length equivalent to fifty per cent. of crossing over.

It should be noted that a *mendel* is not comparable to a

¹ *Proceedings of the National Academy of Science*, 6: 663-670, 1920.

² *Journal of Genetics*, 8: 299-309, 1919.

single short chromosome fifty units long. It is not to be thought of as a fixed portion of any chromosome. The chromosomes are, or course, not to be considered as marked off into fifty-unit lengths. But the result of recombination with a large number of factors is approximately the same as if such were the case. Because it brings out the fact which has not always been fully appreciated, that recombination within a chromosome takes place as easily as between different chromosomes, when the distance between the loci is sufficiently great, the term *mendel* as a measure of chromosome length may have some value.

In the primitive unicellular organisms it is conceivable that the hereditary substances were not located in a mechanism as well regulated as in the higher organisms. As specialization increased, the grouping of factors in chromosomes has undoubtedly been of very great evolutionary significance. The chromosome mechanism has been subjected to natural selection as severely as any external morphological feature and has developed coordinately with sexual reproduction—the one to make recombination possible, the other to make that process orderly.

Although it is largely speculation it seems necessary to believe that there is some functional relation between the factors associated together in a chromosome or portion of a chromosome. There is some evidence for this in the quick and exact return of certain species hybrids to one or the other parental type. Evidently only those individuals resulting from gametes in which crossing over has not occurred are able to live. So far the factors which have been located seem to be placed at random in the chromosomes, and it is impossible to make out any significant relation among them. This in itself may be an indication of an immense number of hereditary determiners which play a part in the organism. For as yet the function of only the relatively superficial factors can be seen. The vitally important ones can not be dispensed with and therefore can not be studied except as the lethal factors show some effect in hybrid combination.

EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

II. HEREDITARY DIFFERENCES IN DURATION OF LIFE IN LINE-BRED STRAINS OF *DROSOPHILA*¹

PROFESSOR RAYMOND PEARL AND SYLVIA L. PARKER

INTRODUCTION

It was shown in the first paper in this series (27)² that there was a marked difference in mean duration of life, and in the form of the l_x curve, between wild-type stocks of *Drosophila* on the one hand and the synthetic quintuple mutation stock on the other hand. It was further made clear that, because of the technique used in the experimental work, there could be no doubt that the basis of this difference must be hereditary and not environmental. Furthermore, Hyde (11) and Pearl (6) have presented evidence for the Mendelian inheritance of this character duration of life.

Given it to be the fact, as the just cited work demonstrates to be the case, that there are hereditary differences within the same species of *Drosophila* in respect of duration of life, the problem which next presents itself is to determine whether *within* a particular strain of *Drosophila* hereditary differences exist, and if so what their magnitude may be, their degree of permanence, etc. In

¹ Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, The Johns Hopkins University, No. 48.

² A word of explanation is necessary as to the method of handling bibliographic references in this series of papers. In the first paper a list of 26 references numbered consecutively from 1 was appended. It is proposed not to duplicate references in any subsequent paper in the same series. Consequently the first *new* bibliographic citation in the present paper is numbered 27. When any reference is made to titles already cited in the first paper in the series, the numbers which they bear in the list appended to that paper will be used. This practice will be adhered to in all subsequent papers in this series of Studies.

short one wishes immediately to get a kind of knowledge for this organism and character similar to that which Johannsen (28, 29) got for the size character of beans from his pure-line work. The first, and in a sense preliminary, investigations on this problem will be presented in this paper. Later in the series we expect to publish much more extended and penetrating evidence on the same problem. Some, however, must be presented early in the series in order to make the account of subsequent experiments intelligible.

It is obvious that in the case of an organism like *Drosophila* it is impossible to have a pure-line in the strict sense of Johannsen. The most that one can do is to have inbred lines, and the most intense degree of inbreeding possible in the premises is by brother \times sister mating. The general plan of the experiments reported in this paper can be outlined as follows:

1. Mate a virgin brother and sister, chosen at random each from the same one of the original 5 foundation stocks (cf. 27).
2. Repeat this for as many pairs as the facilities of the laboratory make possible.
3. Test the progeny of each mated pair separately for duration of life, and form for each group of such progeny a life table.
4. Each such mated pair constitutes the beginning of a line, in which at any time the processes noted under paragraphs 1, 2, and 3 above could be repeated. In this paper will be reported the results of one such repetition.

The general technique of the experimental work has been fully described in the first paper of this series and need not be repeated. It should merely be emphasized again that the environmental conditions in respect of food, housing, temperature (25° C.) and atmospheric conditions were identical for all the flies in the experiments here reported.

DURATION OF LIFE IN DIFFERENT PROGENY GROUPS OUT OF
BROTHER \times SISTER MATINGS

The survivorship data (l_x frequencies) for 7 progeny groups each out of a mating of brother \times sister are exhibited in Table II. All distributions are put on the same basis of 1,000 flies at emergence from the pupal stage. The absolute numbers of flies involved in each experiment are given at the foot of each column. These numbers are

TABLE I
BROTHER \times SISTER MATINGS. FIRST TEST

Lines	Original Stock (Described in (27))	Date of Mating	Date of Emergence
100.....	Old Falmouth	April 8, 1920	April 19-May 3
101.....	" "	April 7, 1920	April 17-May 2
201.....	New Falmouth	April 7, 1920	April 18-May 2
202.....	" "	April 10, 1920	April 20-April 29
300.....	Sepia	April 7, 1920	April 17-May 3
301.....	"	April 6, 1920	April 17-May 3
303.....	"	April 8, 1920	April 18-May 2

TABLE II
SURVIVORSHIP DISTRIBUTIONS OF PROGENY OF BROTHER \times SISTER MATINGS,
BOTH SEXES TOGETHER

Age in Days	Numbers of Survivors up to Indicated Age in Lines No.						
	100	101	201	202	300	301	303
1.....	1,000	1,000	1,000	1,000	1,000	1,000	1,000
6.....	983	993	1,000	689	926	870	882
12.....	937	987	1,000	607	858	727	764
18.....	891	934	952	492	809	602	702
24.....	811	901	943	426	623	441	621
30.....	743	875	857	344	549	342	522
36.....	589	855	790	197	383	255	429
42.....	514	770	600	148	272	205	311
48.....	406	599	505	148	148	130	261
54.....	240	493	381	49	105	75	168
60.....	91	296	219	33	12	31	112
66.....	29	99	133	16	6	12	56
72.....	6	20	10	0	0	2	0
78.....	0	7	10	—	—	0	—
84.....	—	7	0	—	—	—	—
90.....	—	0	—	—	—	—	—
Abs. No. of flies.....	175	152	105	61	162	161	161

smaller than is desirable, but these experiments represent a relatively early stage of the work before the technique of getting maximum progenies for life table work had been perfected. Further it must be remembered that the individuals in any column are the progeny of only one single pair of parents. The source of the lines together with other pertinent data are shown in Table I.

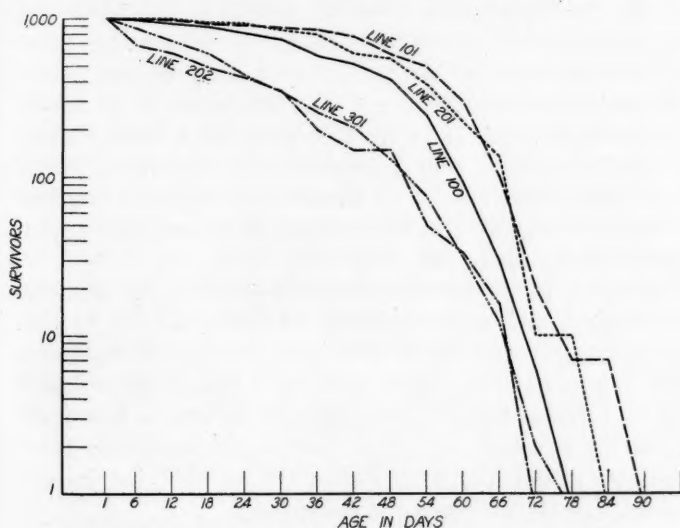


FIG. 1. Survivorship (l_x) graphs for lines 100, 101, 201, 202 and 301.

Five of these distributions are shown graphically in Fig. 1, and their biometric constants are given in Table

TABLE III

FREQUENCY CONSTANTS FOR d_g DISTRIBUTIONS. FIRST TEST

Line No.	Mean Duration of Life (Days)	Standard Deviation (Days)	Coefficient of Variation
100.....	40.45 \pm .84	16.38 \pm .59	40.49 \pm 1.68
101.....	50.02 \pm .85	15.51 \pm .60	31.01 \pm 1.31
201.....	47.40 \pm .99	15.03 \pm .70	31.71 \pm 1.51
202.....	22.04 \pm 1.57	18.18 \pm 1.11	82.49 \pm 7.74
300.....	31.19 \pm .83	15.76 \pm .59	50.53 \pm 2.33
301.....	25.28 \pm .92	17.25 \pm .65	68.24 \pm 3.56
303.....	32.02 \pm 1.07	20.04 \pm .75	62.59 \pm 3.14

III. In calculating these constants, the absolute d_x frequencies, and not the per mille frequencies, were of course used.

From these data it is at once apparent that these progeny groups show distinct, and in some cases decidedly large, differences both in mean duration of life and in the form of the mortality distributions. Lines 101 (Old Falmouth stock) and 201 (New Falmouth stock) show the longest mean duration of life, and they are sensibly identical in the form of the life curve, having regard to the errors of random sampling. The difference in the means for these two lines is 2.62 ± 1.31 days, an obviously insignificant difference, only 2 times its probable error. Similarly these two lines do not significantly differ in absolute or relative variability, the difference between the standard deviation being $.48 \pm .92$.

Line 100 (Old Falmouth stock) has a distinctly and significantly lower mean duration of life than 101 or 201. Comparing it with line 101 the difference in the means is 9.57 ± 1.20 days or approximately 8 times its probable error. The l_x curve lies throughout its course below the lines for 101 and 201. Line 100 is also relatively more variable in duration of life than 101 and 201, but largely because of the difference in the means.

The individuals in line 202 (New Falmouth stock) are the shortest lived of any here dealt with, and the shortest-lived wild-type strain we have as yet isolated. Its mean duration of life is less than half that shown by lines 101 and 201 and only a little more than half that of line 100. Line 202 shows the highest relative variability in duration of life of any of the lines here discussed. It also has the highest absolute variability with one exception (line 303).

Lines 300, 301 and 303 (Sepia stock) are all relatively short-lived lines. 300 and 303 are substantially identical, while 301 has a lower mean approaching that of line 202. These sepia lines are also characterized by high relative variability.

RESULTS OF INBRED RE-TESTS FOR CONSTANCY

During the progress of the experiments described in the preceding section the offspring flies (from original brother \times sister matings) in each of the lines, whose duration of life was being tested, were allowed to mate at random in their bottles, and their progeny removed to form stocks of the several lines. These stocks were allowed to reproduce in stock bottles, all matings being therefore random *within the line*, for a period of about 7 months (cf. Table IV). At the end of that time it was decided to make a re-test of each line to see how it was then behaving relative to duration of life. There was then made, at dates indicated in Table IV, a random selection from each line stock bottle from which a brother and sister pair was bred, and these two individuals were mated to get a set of progeny on which to carry out a second set of life duration experiments. The necessary facts as to line numbers and dates on this re-test are given in Table IV.

TABLE IV
BROTHER \times SISTER MATINGS. SECOND TEST

Line from which Second Selection of Brother and Sister Was Made	Number of Line of Progeny of Second Brother \times Sister Mating	Date of Original Brother \times Sister Mating	Date of Second Brother \times Sister Mating
100.....	104	April 8, 1920	November 6, 1920
101.....	107	April 7, 1920	October 14, 1920
201.....	207	April 7, 1920	October 18, 1920
202.....	208	April 10, 1920	October 14, 1920
300.....	304	April 7, 1920	November 6, 1920
301.....	307	April 6, 1920	October 14, 1920
303.....	309	April 6, 1920	October 14, 1920

The survivorship distributions of the progeny groups of this second brother \times sister mating are given in Table V, and the biometric constants calculated from the observed d_x distributions in Table VI. These tables are for comparison with Tables II and III above.

TABLE V
SURVIVORSHIP DISTRIBUTIONS OF PROGENY OF SECOND BROTHER \times SISTER
MATINGS. BOTH SEXES TOGETHER

Age in Days	Numbers of Survivors up to Indicated Age in Lines No.						
	104	107	207	208	304	307	309
1.....	1,000	1,000	1,000	1,000	1,000	1,000	1,000
6.....	997	1,000	973	833	1,000	862	1,000
12.....	923	950	926	738	870	700	978
18.....	871	926	819	643	870	623	911
24.....	713	917	792	595	674	469	700
30.....	629	901	785	500	478	392	489
36.....	552	860	711	286	435	285	456
42.....	469	777	644	167	261	177	267
48.....	395	686	530	0	152	92	89
54.....	304	595	430	—	109	46	67
60.....	178	488	255	—	0	23	44
66.....	66	264	141	—	—	8	0
72.....	0	83	20	—	—	8	—
78.....	—	8	20	—	—	8	—
84.....	—	0	7	—	—	0	—
90.....	—	—	0	—	—	—	—
Abs. No. of flies	286	121	149	42	46	130	90

TABLE VI
FREQUENCY CONSTANTS FOR \bar{d}_x DISTRIBUTIONS. SECOND INBRED TEST

Line No.	Mean Duration of Life (Days)	Standard Deviation (Days)	Coefficient of Variation
104.....	39.59 \pm .74	18.63 \pm .53	47.06 \pm 1.62
107.....	53.74 \pm 1.07	17.40 \pm .75	32.38 \pm 1.54
207.....	45.34 \pm 1.10	19.97 \pm .78	44.04 \pm 2.03
208.....	25.65 \pm 1.53	14.68 \pm 1.08	57.23 \pm 5.42
304.....	32.09 \pm 1.43	14.43 \pm 1.01	44.97 \pm 3.75
307.....	25.22 \pm .99	16.70 \pm .70	66.22 \pm 3.79
309.....	33.00 \pm .91	12.84 \pm .65	38.91 \pm 2.23

The purpose of this second test was, of course, to see to what extent duration of life was holding constant in the line. During the period between the first and second test the stocks of the several lines had been subjected to varying environmental influences, in particular in relation to temperature, the stock bottles having been kept at room temperature, which varied rather extensively. Did the lines after 7 months have the same characteristic life curves that they exhibited on the first test? Allowing 12

days from generation to generation in the case of flies reproducing freely at random in stock bottles, the interval elapsing between the first and second tests would cover roughly almost 18 generations. This is a long period and affords abundant opportunity for change in the average genetic constitution of the population.

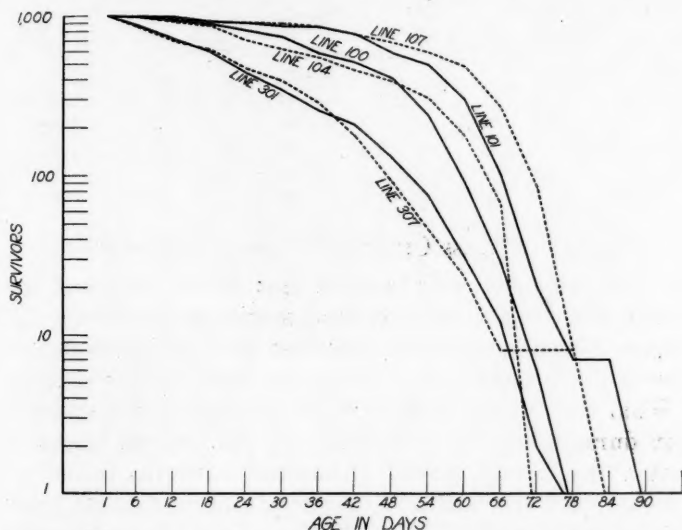


FIG. 2. Comparing the l_x lines of the first and second inbred tests. of lines 101, 100 and 301.

An examination of Tables V and VI and Fig. 2 shows at once, in a general way, that the characteristic features of the several lines in respect of duration of life did in fact hold remarkably constant during this period. A more precise comparison of the means is made in Table VII.

There can be no question of the substantial constancy of these lines, over the period covered in the tests in respect of duration of life. The l_x curves run well together till the upper end of life is reached, where, because of the small numbers involved, there is some irregularity. In no case is the difference between two comparable means, as shown in Table VII, as much even as three times its prob-

able error, nor is there any certainly significant change in variability having regard to the probable errors of the differences involved.

TABLE VII

DIFFERENCES IN MEAN DURATION OF LIFE BETWEEN THE FIRST AND SECOND
INBRED TESTS OF THE SEVERAL LINES

Corresponding Lines (Mean of Second Test Minus Mean of First)	Difference of Means (Days)	Diff. P. E. Diff.
104-100	- .86 \pm 1.12	.77
107-101	+ 3.72 \pm 1.37	2.72
207-201	- 2.06 \pm 1.48	1.39
208-202	+ 3.61 \pm 2.19	1.65
304-300	+ .90 \pm 1.65	.54
307-301	+ .06 \pm 1.35	.04
309-303	+ .98 \pm 1.40	.70

RESULTS OF MASS CULTURE RE-TESTS FOR CONSTANCY

The point may well be made that in the re-tests of the lines described in the preceding section an additional element is introduced in the fact that the flies for the re-test were the progeny of a second brother \times sister mating. What one wishes to know is: what degree of constancy in duration of life is exhibited by the general stocks in each line, mating purely at random, after the initial selection and inbreeding? We wish now to present some data on this point. Table VIII gives the biometric constants for this material. Mass culture re-tests have been made on two of the original lines, 100 and 101. These mass culture re-tests were made in two ways as follows:

(a) From the stock bottles of the line to be tested a large sample of progeny was taken at random each day as the flies emerged from the pupal stage, and these progeny flies were put in small bottles for a duration of life experiment in the usual way described in (27).

(b) From the stock bottles of a particular line to be tested a number of virgin flies (usually 8 to 10 of each sex) were taken at random immediately upon emergence, and mated as a group in a mating bottle. The progeny from this sample was then removed, upon emergence, to small bottles and a regular duration of life test carried as described in (27).

TABLE VIII
FREQUENCY CONSTANTS FOR MASS CULTURE RE-TESTS. ORIGINAL LINES

Line No.	Test	Dates of Emergence	Numbers of Flies	Mean (Days)	Standard Deviation (Days)	Coefficient of Variation
100.	Mass Culture	1920 Sept. 25-Oct. 21	433	33.05 ± .76	23.48 ± .54	71.05 ± 2.31
	Original brother × sister	1920 Apr. 19-May 3	175	40.45 ± .84	16.38 ± .59	40.49 ± 1.08
Difference		5 mo. 12 days	—	— 7.40 ± 1.13	+ 7.10 ± .80	+ 30.56 ± 2.68
101.	Mass Culture A	1920 Sept. 25-Oct. 21	473	53.09 ± .70	22.53 ± .49	42.44 ± 1.09
	Mass Culture B	1921 Mar. 18-Apr. 4	124	48.53 ± 1.02	16.76 ± .72	34.54 ± 1.65
	Original brother × sister	1920 Apr. 17-May 2	152	50.02 ± .85	15.51 ± .60	31.01 ± 1.31
Difference OA		5 mo. 13 days	—	+ 3.07 ± 1.10	+ 7.02 ± .77	+ 11.43 ± 1.70
Difference OB		10 mo. 29 days	—	— 1.49 ± 1.33	+ 1.25 ± .94	+ 3.53 ± 2.11

It is at once apparent that the mass re-tests on line 101 gave extremely satisfactory results as to constancy of duration of life in the line, after intervals of approximately 5 and 11 months. The mean value for either the *A* or the *B* test does not significantly differ, having regard to its probable error, from the mean shown on the original test at the start of the line. The mean of the *A* mass re-test almost exactly agrees with that of the second inbred test of the same line, as given in Table VI.

In the case of line 100, the mass re-test after 5½ months approximately does not give such close agreement. The mean is significantly lower, the difference being 6.6 times its probable error. No explanation of this result is, as yet, forthcoming, but it probably means no more than lack of genetic purity in the line. It is, however, interesting to note that the sense of the change is in the same direction as that in which line 100 in general differs from line 101, which we regard as our most typical wild-type line in respect of duration of life. That is, line 100 is, as compared with 101, a shorter-lived line. Its mass culture re-test is still shorter lived.

The variability in respect of duration of life, whether measured in absolute or relative terms, is uniformly higher and in two cases out of the three by a significant amount in the mass culture than in the original inbred tests. This is, of course, exactly what would be expected on general genetic grounds. One brother \times sister mating, as has been shown by Pearl (30), Jennings (31) and others, reduces the heterozygosis in the strain by only 50 per cent. It is interesting to note, in connection with the explanation suggested above for the difference in the means in the case of line 100, that the variability in the mass re-test on that line is very much higher than in the original inbred test.

A mass re-test was carried out on two of the lines from the second brother \times sister matings. The results from these experiments are presented in Table IX.

TABLE IX
FREQUENCY CONSTANTS FOR MASS CULTURE RE-TESTS. TWICE INBRED LINE

Line No.	Test	Date of Emergence	Numbers of Flies	Mean (Days)	Standard Deviation (Days)	Coefficient of Variation
107	Mass Culture A	1921 Apr. 19-Apr. 22	1,338	49.74 ± .25	13.69 ± .18	27.52 ± .54
107	Second brother × sister S	1920 Oct. 25-Nov. 4	121	53.74 ± 1.07	17.40 ± .75	32.38 ± 1.54
101	Original brother × sister O	1920 Apr. 17-May 2	152	50.02 ± .85	15.51 ± .60	31.01 ± 1.31
Difference SA		6 mos. 9 days	—	4.00 ± 1.10	3.71 ± .77	4.86 ± 1.63
Difference OA		11 mos. 27 days	—	.28 ± .88	1.82 ± .96	3.49 ± 1.42
309	Mass Culture A	1921 May 18-25	468	34.04 ± .34	11.02 ± .24	32.38 ± .79
309	Second brother × sister S	1920 Oct. 25-Nov. 1	90	35.00 ± .91	12.84 ± .65	38.91 ± 2.23
303	Original brother × sister	1920 Apr. 18-May 2	161	32.02 ± 1.07	20.04 ± .75	62.59 ± 3.14
Difference SA		6 mos. 28 days	—	1.04 ± .97	1.82 ± .69	6.53 ± 2.37
Difference OA		13 mos. 1 day	—	2.02 ± 1.12	9.02 ± .79	30.21 ± 3.24

The substantial constancy of line 101, in both mass and inbred tests, is evident. In respect of variability the line behaved somewhat like 303 discussed below.

In line 303 again the constancy of the line in respect of mean duration of life is as definite as could be expected. Over periods of approximately 7 and 13 months, the mean duration of life has not sensibly changed, having regard to the probable error involved. The results respecting variability are somewhat anomalous. Both the second inbred and the mass re-test show variability of a distinctly lower order than was exhibited by the progeny of the original brother \times sister mating. It seems probable that the original test by accident gave a variability result higher than was really characteristic of the line. But the mass culture re-test exhibits a lower variability, not certainly significant, to be sure, than the first test on line 309. Of course it is to be expected that with continued brother \times sister mating the variability of mass cultures from the line would come nearer and nearer to that of a further inbred lot of progeny from the same line. Probably the results of Table IX are an expression of the realization of such expectation, obscured by the fact that the numbers are small and the errors of sampling consequently relatively large.

DISCUSSION AND SUMMARY

The data presented in this paper appear to demonstrate, with comprehensiveness and accuracy, three broad facts.

A. That there exist in a general population of *Drosophila melanogaster* (or its mutants) genetic differences in respect of duration of life.

B. That these genetic differences are capable of isolation, by appropriate selection and inbreeding.

C. That within an even moderately inbred line, the genetic differences in duration of life remain constant over periods of at least 10 to 25 or more generations.

These facts, based upon the determination experimentally of the duration of life of 3,039 individual flies in 18 experiments, under constant environmental conditions, place this character "duration of life" in the category of genetically definite and workable characters, and indicate that it will just as well repay careful analytical study as the characters more usually dealt with. Furthermore, duration of life is a character of great general biological significance.

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SHORTER ARTICLES AND DISCUSSIONS

NOTE ON A CASE OF HUMAN INBREEDING¹

THROUGH the kindness of a friend the following pedigree is presented. It is that of a family of English stock, which has been in this country since the early eighteenth century, and during that time has been one of the principal families of a rural community.

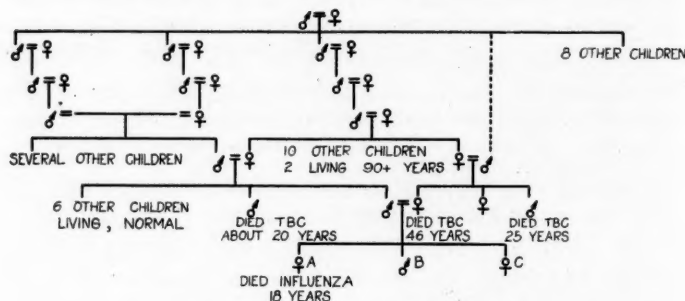


FIG. 1. Pedigree of an inbred family.

To quote from my correspondent's letter, "A was a fine young girl. She had graduated from high school but did not go to college as her mother had died in the summer and she wished to take charge of the home. B is about 16 years old. A splendid young man, bright and apparently healthy. He is in school standing about average. C is 10 years old or thereabouts. An exceptionally bright child and one that is very much alive and full of spirit."

Assuming that the line of descent represented in the figure by a broken line, indicating that the number of generations is not known, includes the same number of generations as the other lines the coefficients of inbreeding² for the children in the last

¹ Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 41.

² Pearl, "Studies on Inbreeding," I-VIII, AMERICAN NATURALIST, 1913-17.

generation (viz., A, B, and C) are as follows:

$$\begin{array}{ll} Z_1 = 0, & Z_4 = 25, \\ Z_2 = 25, & Z_5 = 34.37, \\ Z_3 = 25, & Z_{T_5} = 27.1, \end{array}$$

i.e., in five generations of ancestry the inbreeding is about a quarter of the possible maximum.

There is no deleterious effect of inbreeding apparent in this pedigree. The three children in the last generation, the most inbred of any, show no signs of abnormality. In their father's fraternity, for which $Z_1 = Z_2 = Z_3 = 0$; $Z_4 = 12.5$; $Z_{T_4} = 4.1$, or in four generations of ancestry there is $\frac{1}{25}$ of the possible maximum inbreeding, one of eight died of tuberculosis; the other seven have attained adult age. In the mother's fraternity, for which $Z_1 = Z_2 = Z_3 = 0$; $Z_4 = 6.25$; $Z_{T_4} = 2.0$, two out of the three have died of tuberculosis. The least inbred, therefore, show the greatest susceptibility to tuberculosis. The numbers are, of course, too small to draw any certain inference, but so far as they go, they accord best with the view that there is no harmful effect of inbreeding per se.

JOHN RICE MINER

ON COLOR VARIATIONS IN CHITONS

THE question was raised by Bateson ("Materials," 1894, p. 307) as to whether variation occurring in serial parts whose repetition is not strictly speaking of a metamerie sort, would be found to simultaneously affect each of the parts involved in such a series. With this point in mind he examined a collection of chitons, the 8 shell plates of these animals providing an excellent opportunity for such observations. He found color variations affecting all the plates of an individual to be of rather rare occurrence, but that plates 2, 4 and 7 seemed, on the other hand, to exhibit a decided tendency to vary together (in several species of *Chiton*).

Although the problem of metamerism, so far as it concerns variation, has perhaps lost some of its original attractiveness, I have thought it worth while to point out that in *Chatoppleura* several curious types of shell variation are apparent, involving either simultaneous variation throughout the series or variation in a single shell-valve alone, or both.

The commonest type of color pattern, in *Chaetopieura apiculata*, is one which involves a double band of blackish or grayish pigment running the length of valves 2 to 8, the bands joined on 2 and on 8 by continuous semicircular blotches (cf. Fig. 1, *d*).

In 3 out of 219 specimens, however, a central dark stripe, clearly marked on valves 2 to 8 inclusive, accompanied a much fainter double band extending to valve 1 (Fig. 1, *b*), and made up of regular triangular grayish blotches on the posterior borders of valves 2 to 7. In one case, a bright central band of white

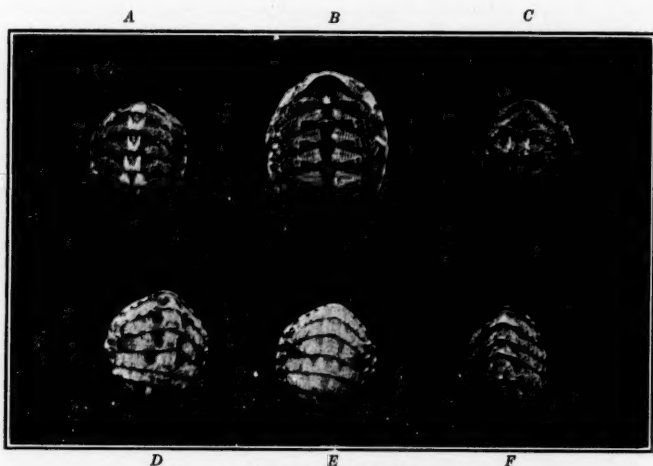


FIG. 1. *Chaetopieura apiculata* ($\times 2$).

was marked by a median grayish blotch on valves 3 to 7 (Fig. 1, *a*); a paler example of the same kind is shown in Fig. 1, *e*.

These are instances where variation from the more usual color type clearly has taken place simultaneously in the whole series of valve-plates, this condition being seen not only in the form of the central stripe, but also in the shapes of the individual pigment blotches comprised in the double band (cf. Fig. 1, *a* and *b*), as well as in a few cases where three small but distinct pigment flecks were noted on the lateral field of each plate.

In addition, however, two sorts of pattern variation occur which are quite different from the foregoing. In three instances a definite yellow or orange central blotch appeared on valve 2, and nowhere else (Fig. 1, *c*). And in five further instances there was found a marked blackish blotch at either lateral margin of valve

4 (Fig. 1, *d, e*). In two further cases, this type of lateral marking was continued in the form of less distinct marginal blotches on valve 3. The marginal blotches on valve 4 may accompany an otherwise "normal" pigment pattern (10 examples in 219 examined; Fig. 1, *d*), or may be present where there is evidence of a tendency for the formation of a distinct axial stripe (five examples; Fig. 1, *e*).

It is evident, then, that in Chitons color pattern variations may occur in such a way as to affect single valves only (and, in *Chatopleura*, specifically valve 2 or 4); and either quite independently of this type of variation or accompanying it, may also affect all valves in the series simultaneously. Such variations are quite independent of age.

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FUGITIVE NET-VEINING IN THE CICADA (HEMIPTERA)

TILLYARD has¹ lately noted¹ that, besides the chitinized veins which serve for the support of the insect wing, there exist in some cases at least fugitive blood-veins during the expansion of the wing, which later collapse and more or less completely disappear when the wing dries. In the Lepidoptera 1st A and the base of M are veins of the same character, and possess tracheæ like other longitudinal veins in that order. In every particular except the absence of chitinization these appear to be true veins, and in forms where the veins are provided with special series of setæ, as in *Acræa*, they are often similarly supplied.

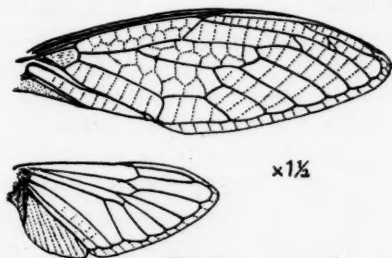


FIG. 1.

In watching a cicada expand, recently, I saw appear, as the

¹ *Proc. Linn. Soc., New S. Wales*, 44, 621; 1919.

expansion approached completion, a regular system of blood-veins in the spaces between the permanent veins. These show plainly only in the few minutes when the wing has become partially transparent, but in the adult wing they produce a characteristic waviness of the membrane, and a few of them may be seen in a favorable light as faint white lines. The arrangement is perfectly definite: the narrow cells are filled by a series of simple, evenly spaced, cross-veins, while in cells R, 1st M_2 and M they form a double series of cells alternating with each other. On the narrow margin beyond the ambient vein they are evenly spaced, the regular longitudinal veins each ending opposite the middle of a marginal cell. Toward the costa there are two veins opposite each definitive cell, while opposite cells M_3 and M_4 there are three, and opposite cell Cu_1 there appear to be four. The margin of the hind wing is similar, but the disc of the wing was not observed. In the large triangular anal cell (3d A_1), instead of cross-veins there is a series of closely spaced parallel longitudinal veins, which remain visible in the dried wing.

It seems possible that these structures are the relic of a net-veining such as occurs in the Neuroptera. The different arrangement in the anal region is especially suggestive, as it would correspond to the plaited portion of the wing in the Orthoptera, where there exist numerous parallel longitudinal veins.

The figure is drawn from memory so far as the fugitive veins are concerned, checked up by the few that could be traced in the dry wing; it can be trusted only approximately.

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